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EXPERIMENTAL STUDIES ON THE CHOICE OF OVIPOSITION SITES BY TWO SPECIES OF *CHORTHIPPUS* (ORTHOPTERA: ACRIDIDAE)

By J. C. B. CHOUDHURI

Department of Zoology, University of Saugar, Sagar, India

(With 5 figures in the text)

It has been observed that most acridid species have restricted oviposition sites. In some species the soil relation is very pronounced while in others it is not so well marked or may be altogether absent. Vestal (1913), Smith (1915), Severin & Gilbertson (1917), Criddle (1918, 1933), Rubtzov (1935), Shotwell (1935), Weddel (1937), Zimin (1938), Watson & Bartley (1940), Clark (1949), Waloff (1950) and Richards & Waloff (1954) have described the selection of egg-laying sites in grasshoppers inhabiting fields, meadows, pastures and sandy heaths. Some workers like McClung (1899), Rubtzov (1935), Knutson (1937), Iseley (1938) and Professor George J. Spencer (private communication) have also attempted to study experimentally and to analyse the factors responsible for such selection in grasshoppers. Experimental studies on the selection of oviposition sites by several locust species have been made by Johnston & Maxwell-Darling (1931), Faure (1932), Kennedy (1949), Znamenskii (1951) and Choudhuri (1956a, b). Observations on the experimental studies on the choice of oviposition sites by two common British grasshoppers, *Chorthippus parallelus* (Zett.) and *C. brunneus* (Thunb.) are reported here.

METHODS

All the laboratory experiments were performed in cages ($21 \times 16 \times 19$ in.) made of wood with glass sides, hardboard bottom and trap-door on the front. On the bottom half of the front side of the cage a strip of board was placed which could be removed to push in or take out sand dishes from the cage. About $1\frac{1}{2}$ in. from the bottom a groove was made on three sides of the cage, except the front, to slide in the false bottom. This was also made of hardboard with several holes arranged in four rows to hold glass dishes (2×1 in.) containing soil. The cage was lighted by a 60 W electric lamp, switched on during daytime and off at night.

Nymphs of the two species of grasshoppers, mostly late instars, were collected from field and were reared in standard (Watkins & Doncaster) celluloid cages. When the adults were about a week old they were used for the experiments. Insects were fed on *Holcus* sp. or *Agrostis* sp.; grass was always kept fresh by standing it in small glass vials filled with water. In most experiments about twenty-five pairs of mature insects were used; when more insects were used their numbers have been stated.

Common builder's sand was used to make different types of soils. The sand was first sieved through a standard sieve of 20 mesh and then dried in an electric oven at 110° C for 5 h. After cooling the sand for some time, the dishes were filled with it. A known quantity of water was added to each dish by means of a burette to make sand of different moisture contents. The following arbitrary scale was followed in defining the moisture content of sand:

1. Moist sand—10 ml of water added to 136 g of dried sand. In this only the top few millimetres were moistened with water.
2. Wet sand—20 ml of water added to 136 g of dried sand. The sand was well soaked with water.
3. Sodden sand—30 ml of water added to 136 g of sand. The sand was nearly saturated with water.

The moisture content determinations were done by the oven-dry method.

To prepare sand of different compactions the following procedure was adopted. The compact sand was prepared by alternate wetting and drying in the oven; it was hard and firm. The compressed sand was prepared by ramming the sand with a rubber bung; it was noted that pressing was always effective if the sand was slightly moistened. No treatment was necessary for the loose sand except that occasionally the dish was gently tapped so as to keep the sand particles loose. Finally, bigger lumps of sand were broken into small pieces which were closely packed into the dish to make lumps of sand.

To get sands of different particle size the sand was first sieved through a very coarse gauze to remove big lumps of sand and litter. It was then sieved through a 20 mesh gauze and fairly big particles which were retained were collected to make up the 'coarse sand'. The sifted sand was again sieved through 30 and 40 mesh sieves; the sand retained by the 40 mesh sieve was used as 'medium sand'. Finally, the sand was sieved through a 60 mesh gauze which sifted out 'fine sand'. The measurements of the soil particles were: coarse sand—2·0-1·0 mm, medium sand—0·75-0·4 mm, fine sand—0·35-0·15 mm.

To prepare sand of different pH values McIlvain's buffer solution was used (Vogel 1948, p. 809). After washing the sand under running water for several hours to remove most of the organic matter, the sand was placed in an 800 ml conical flask and the solution of the required pH was poured into it. The sand was thoroughly stirred in the liquid and kept overnight. The excess liquid was drained off and the sand was slightly warmed to evaporate water till it acquired a moist consistency. Treatments at pH 4·4, 5·4, 6·8, 7·8 and 8·0 were prepared. The neutral sand (pH 6·8) was obtained by washing the 'stock sand' several times in distilled water. The determinations of pH values were carried out by the B.D.H. barium sulphate soil testing outfit using B.D.H. soil indicator and the universal indicator.

Thermocouples and thermometers were used to measure temperature of the sand and inside the cage. Edney's paper hygrometers were used for measuring relative humidity.

The determinations of soil compactions were carried out with a soil penetrometer devised for the purpose. The penetrometer (Fig. 1) consists of a brass cylinder (C), 15 in. long and 3 in. in diameter, closed at both ends. The cylinder has a window (W) leaving about $\frac{1}{2}$ in. at the upper and about 2 in. at the lower ends respectively; it rests on a tripod (T). A brass guide-rod (Gr) $\frac{1}{4}$ in. in diameter is passed through the cylinder; the lower end of the rod is threaded to hold the probe; the upper end

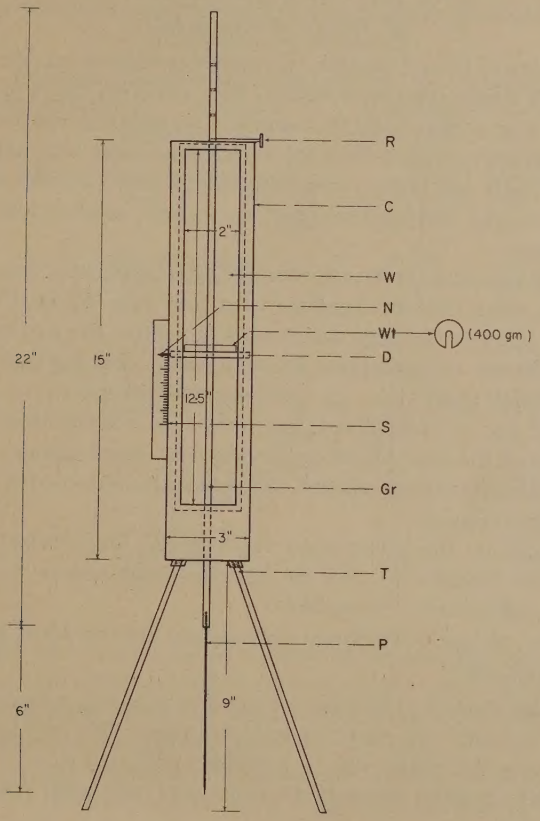

Fig. 1. The soil penetrometer; for details see text.

of the rod is provided with equally spaced holes in which a retainer (R) is inserted. At the end of the rod a thin circular metal disc (D) about 0·15 in. in thickness and slightly smaller than the diameter of the cylinder in which it slips smoothly is fixed. The disc acts as a platform for the falling weight and bears a needle pointer (N) which is used to read penetration of the probe against the scale (S) attached to the cylinder. The scale is marked in inches. The probe (P) is a narrow steel rod, 6 in. long and 0·1 in. in diameter; its upper end is threaded and fits into the guide-rod and the lower end is conical and pointed.

A small lead disc (Wt) about 2 in. in diameter weighing 400 g is used as the standard weight. It is grooved on one side through which it slides on the guide-rod; when dropped from a standard height on the platform it drives the rod which pushes the probe into the soil. The penetration of the probe after each impact is directly read from the scale.

SOIL SELECTION EXPERIMENTS

(*a*) *Design of experiments*

At the beginning of the season some preliminary experiments on soil types, soil moisture and soil compaction were carried out. Different types of soils were collected from the grasshopper habitats—sandy loose soil from the anthills of *Lasius flavus* (Faby.) occurring within the habitat, hard soil from bare patches, soil with carpet of grass (turf) and lastly common builder's sand. Similar sand of varying moisture contents and compactions (dry, moist, wet, sodden, loose, pressed and compact) was used.

Glass dishes containing the treatments and their replicates were placed in the cage at random using random number tables, and exposed for 15 h. During an experiment the lamp in the cage was always on. After the exposure period, the dishes were taken out and examined for empty holes and egg-pods. Food (grass) was offered in small glass vials. In preliminary experiments the position of the food in the cage was not considered, but when it was found that the location of the food influenced the selection of egg-laying sites, precautionary measures were taken in the final factorial experiment. Experiments were carried out in separate cages with mature females.

On the findings of the preliminary experiments more critical and factorial experiments were planned to find the optimal requirements for oviposition of *Chorthippus parallelus* and *C. brunneus*.

Results of sets of four preliminary experiments are tabulated in Table 1. The conclusions drawn are:

1. *C. parallelus* showed preference for egg-laying in soil collected from anthills but no such preference was observed in *C. brunneus*. The soil from anthills was moist; this may be the reason why *C. parallelus* preferred it.
2. *C. parallelus* reacted strongly to moist and wet sand while *C. brunneus* preferred dry sand.
3. Both species, especially *C. brunneus*, laid fewer pods in sodden sand.
4. *C. brunneus* showed some preference for hard soil but no such preference for soil compaction was observed in *C. parallelus*. (The data in experiment No. 4 were tested statistically. The calculated value of $\chi^2 = 12{\cdot}5$ ($P > 0{\cdot}05$) which suggests that egg-pods were not deposited at random. It seems that soil structure has some influence on oviposition.

The preliminary experiments indicated that the moisture content of soil besides other soil factors influence the selection of the egg-laying site, and they proved useful in designing further experiments of a more critical nature. The factors

studied were: moisture content, compaction, particle size, soil reaction and temperature.

These factors were investigated at different levels by using sand, and each of them was studied separately one at a time. Later factorial experiments were designed to study the combined influence of these factors on oviposition.

Table 1. *The number of egg-pods laid by* Chorthippus parallelus *and* C. brunneus *in different soil treatments*

In this and subsequent tables, percentages are given in parentheses

Experiment	Treatments	*C. parallelus*	*C. brunneus*
1	Builder's sand	11 (17·8)	41 (46·1)
	Soil from anthill	40 (64·5)	13 (14·6)
	Soil from bare patch	9 (14·5)	35 (39·3)
	Turf	2 (3·2)	0
	Total	62	89
2	Soil from anthill	30 (73)	35 (40)
	Builder's sand	11 (27)	53 (60)
	Total	41	88
3	Dry sand	28 (16)	85 (43)
	Moist sand	70 (41)	42 (22)
	Wet sand	60 (35)	38 (20)
	Sodden sand	14 (8)	31 (15)
	Total	172	197
4	Dry loose (flattened)	0	5 (12·5)
	Dry loose (mound)	0	0
	Dry pressed	0	11 (27.5)
	Dry compact	0	10 (25)
	Dry lumps	0	9 (22·5)
	Moist sand	10 (100)	5 (12.5)
	Total	10	40

Experiments were carried out in a constant-temperature room (30° C and R.H. 65%). A small amount of water (5-6 ml) was added to the sand to make it slightly moist in experiments where the influence of oviposition response to sand of different compactions and particle sizes were studied.

In the preliminary experiments trial oviposition holes were found. There were empty holes of half or full length which were never covered up as were the holes where laying took place. It was thought that the number of these trial holes might be used as an index to measure the degree of preference for different types of soils, and a record of empty holes, half drilled or full length, was kept. The occurrence of high numbers of empty holes in a dish with a low number of pods suggests that gravid females searching for egg-laying sites tried the sand several times but did not find it suitable for oviposition.

(*b*) *Influence of moisture content*

In experiment No. 2 it was observed that both species showed some response to the moisture content of sand. This experiment was designed to determine the

oviposition response in sands with a range of moisture content. Four treatments of sand, dry, moist, wet and sodden, were offered for egg-laying. It was found that the loss of water from the sand dishes by evaporation during the exposure period was negligible.

The data are given in Table 2. Both species laid a low percentage of egg-pods in sodden sand. *C. parallelus* preferred moist sand since the number of empty holes

Table 2. *The number of egg-pods and empty holes in sand of different moisture content*

	Sand				Totals
	Dry	Moist	Wet	Sodden	
C. parallelus					
Egg-pods	6 (5)	55 (44)	39 (31)	26 (20)	126
Empty holes	?	4 (12·6)	15 (46·8)	13 (40·6)	32
C. brunneus					
Egg-pods	77 (55)	30 (21)	21 (15)	13 (9)	141
Empty holes	?	11 (22·9)	13 (27·1)	24 (50)	48

was least and the number of full ones was maximal. *C. brunneus* used moist sand for egg-laying more than wet and sodden sand but preferred to lay in dry sand. Both species show a tendency to dig more trial holes as the moisture content of sand increases, and this is more pronounced in *C. brunneus*.

(*c*) *Influence of compaction*

In a preliminary experiment, *C. brunneus* showed some tendency to lay more egg-pods in pressed or compact sand. *C. parallelus* did not show any such preference, but the absence of any such response may possibly be due to treatments which were not properly controlled. In the present experiment three well-controlled treatments of sand, loose, pressed and compact, were offered for egg-laying. The mean penetrations observed with the soil penetrometer were: loose sand 1·6 in., pressed 1·3 in., compact 1·0 in.

Table 3. *The number of egg-pods and empty holes in different compactions of sand*

	Sand			Totals
	Loose	Pressed	Compact	
C. parallelus				
Egg-pods	42 (35)	42 (35)	36 (30)	120
Empty holes	9 (25·7)	10 (28·6)	16 (45·7)	35
C. brunneus				
Egg-pods	23 (17·8)	45 (34·9)	61 (47·3)	129
Empty holes	19 (48·8)	13 (33·3)	7 (17·9)	39

The data are tabulated in Table 3. *C. parallelus* did not respond to the compaction of sand for egg-laying, and its empty holes were also distributed uniformly in all the treatments. *C. brunneus* reacted to compact sand in which the maximum number of egg-pods was laid (47·3%) with least number of empty holes. There

was a tendency to deposit fewer egg-pods in pressed and loose sand which were tried several times, since more empty holes were present in those two treatments. It seems, therefore, that the compaction of sand influenced the oviposition in *C. brunneus* and not in *C. parallelus*.

(*d*) *Influence of particle size*

To observe the effect of soil texture on selection of oviposition site three grades of sand were made up of different particle sizes, coarse, medium and fine. The data obtained are given in Table 4. The figures show that *C. parallelus* laid most egg-pods in coarse sand while *C. brunneus* did so in medium sand. In both species there were fewer empty holes in medium sand. It will be also noted that *C. parallelus* seems to have made several trials in fine sand but it was not used for egg-laying. In *C. brunneus* there was not much difference in the number of empty holes found in fine and coarse sand.

Table 4. *The number of egg-pods and empty holes in sand of different particle sizes*

	Sand			
	Fine	Medium	Coarse	Totals
C. parallelus				
Egg-pods	8 (8)	34 (37)	51 (55)	93
Empty holes	20 (48·8)	8 (19·5)	13 (31·7)	41
C. brunneus				
Egg-pods	32 (30)	57 (53)	18 (17)	107
Empty holes	16 (35·5)	9 (20)	20 (44·5)	45

(*e*) *Influence of soil reaction*

Sand of pH values 4·4, 5·4, 6·8, 7·8 and 8·0 were used. The data are presented in Table 5 which show that no egg-pod was laid in sand of pH 4·4. Soil of such high

Table 5. *The number of egg-pods and empty holes in sand of different pH values*

	pH 4·4	pH 5·4	pH 6·8	pH 7·8	pH 8·0	Totals
C. parallelus						
Egg-pods	0	15 (17·3)	24 (27·6)	23 (26·4)	25 (28·7)	87
Empty holes	7 (26·9)	5 (19·2)	4 (15·4)	6 (23·1)	4 (15·4)	26
C. brunneus						
Egg-pods	0	25 (19·4)	32 (24·8)	37 (28·6)	35 (27·2)	129
Empty holes	10 (27·1)	7 (18·9)	6 (16·2)	8 (21·6)	6 (21·6)	37

acidity does not occur normally in nature except in the vicinity of some sulphur springs, particularly in grasshopper habitats. The frequency of pods laid in sand of pH 5·4, 6·8, 7·8 and 8·0 was fairly uniform and no distinct preference was revealed. Highly acid sand tends to become sticky, and probably for this reason no pod was laid in it. This negative effect may be attributed to the structural changes in the sand rather than to the influence of its pH. Hence, it appears that soil reaction does not influence oviposition of the insects under study.

(*f*) *Influence of soil temperature*

In the field, *C. parallelus* and *C. brunneus* usually deposit their egg-pods on ant-hills or in bare patches, where the surface temperature is usually higher than the surrounding grass-covered soil. A cage experiment was designed to study the influence of surface soil temperature on the oviposition responses. A false wooden floor was fixed in a glass cage 24 × 24 × 25 in. At the centre of the board a square

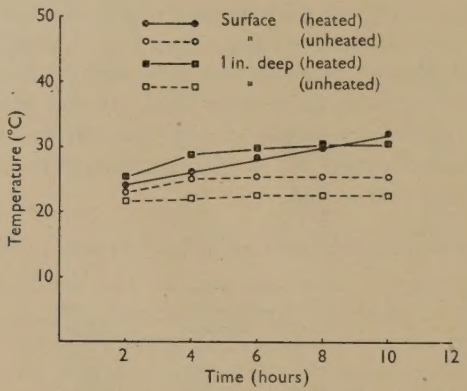

Fig. 2. Temperature record of heated and unheated sands.

hole was made in which a tightly fitting piece of hardboard was placed. Sixteen holes about 1 in. in diameter and 1½ in. apart were drilled in it, arranged in four rows of four. The heating devices made of two concentric asbestos tubes were installed in alternate rows. A heating element was coiled around the inner tube and was covered by the outer tube. These tubes were clipped to the wooden supports which were screwed to the central board. Terminals were connected to the mains through a step-down transformer. A rheostat controlled the current, and it was found that about 3 A were sufficient to raise the temperature of sand to 32-34° C.

Sand tubes measuring about 6 × 1 in. were filled with sand and a small amount of water was added to each tube. Four tubes in alternate rows were heated and the others were kept cold. The tubes were heated for four hours before commencing the experiment. The mean temperature readings are shown in Fig. 2.

The data obtained are given in Table 6 and were subjected to analysis of variance, which showed that one of the main factors, heat, is significant. This suggests that both species prefer laying in warm sand. The failure of the interaction term in the analysis to attain significance suggests that the two species react alike.

On the basis of these observations another experiment was designed to find the range of soil temperature preferred for oviposition. A glass tank 42 × 18 × 20 in. was filled to a depth of about 6 in. with sand sieved through a 20 mesh sieve. On

one side of the tank a heating mat 6×6 in. was buried in the sand and connected with a thermostat. Seven thermometers were placed 6 in. apart in a row on the surface. The placing of the thermometers was such that eight temperature zones were available within the tank, six between thermometers and the first and last

Table 6. *The number of egg-pods laid by* C. parallelus *and* C. brunneus *in heated and cold tubes*

	Heated tubes (Surface 32° C)	Cold tubes (Surface 25° C)	Total egg-pods
C parallelus	90	37	127
C. brunneus	28	15	43
Totals	118	52	170

end zones between the sides of the glass tank and the thermometer. Four 60 W electric lamps were placed outside the cage and about 2 ft away from it, one on each side to have an equal illumination inside the cage. The experiment was carried out in the constant temperature room. The sand was heated for two days before commencing the experiment in order to get a steady temperature gradient on the sand surface. Temperatures at the sand surface were noted down at regular intervals and averaged 26·5° C, 27·0° C, 27·5° C, 28·2° C, 30·7° C, 31·0° C, and 35·3° C.

Seventy-five gravid females of *C. parallelus* and ninety females of *C. brunneus* were released in the cage and regularly fed on grass. At the end of three weeks the egg-pods laid in the different temperature zones were collected, counted and identified. The maximum number of pods was laid by both species between 28 and 35·3° C, and only very few pods were deposited in sand below 28° C, suggesting that both species have a preference for depositing their egg-pods in warm sand. The coefficients of correlation calculated from the data gave values of $r = 0{\cdot}75$ and 0·89 for *C. paralleus* and *C. brunneus* respectively. Both coefficients are significant at 1% level. A positive correlation between the number of pods laid and the temperature of the sand was established (Fig. 3). The results suggest that the temperature of the surface soil has a significant effect on the selection of egg-laying site, and raise the question whether gravid females are primarily attracted to the warm spots for basking rather than for oviposition. To clarify this point the following experiment was planned.

Two wooden trays (14·5 × 10 × 3·6 in.) were placed in the tank used in the previous experiment; one was kept cold and the other was equipped with a heating mat (6 × 6 in.) and both were filled with moist sand. The portion of the floor which was not occupied by trays was covered with hardboard so as to raise the floor to the sand level. Two electric 60 W lamps were placed inside the cage not directly over the trays. From pilot experiments it was found that the surface temperature of the hot sand could be maintained close to 35° C during the observation period by switching the heating mat alternately on and off at two-hour intervals.

Fifty mature females of *C. parallelus* and *C. brunneus* were released in the cage. Their distribution in the cage was recorded at two-hour intervals from 10 a.m. to

10 p.m. At the end of the day's observations, the light and heating mat were turned off and were turned on again the following morning. The average data for the 7 days' observations are presented in Fig. 4.

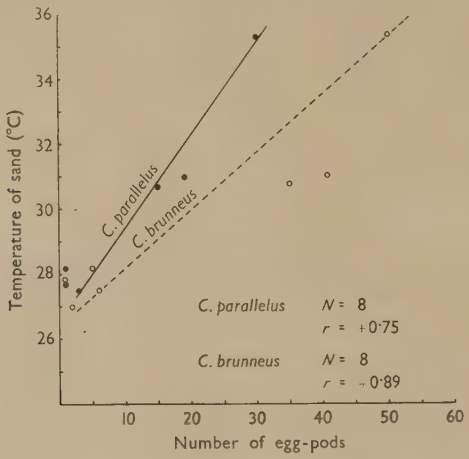

Fig. 3. Scatter diagram of the positive correlation between the egg-pods laid and the temperature of the sand.

Fig. 4. The frequency distribution of insects on various substrata.

The distribution curves show that the number of insects seen on the board was high during morning hours, when they were seen mostly sitting or basking, but gradually fell as the temperature inside the cage was raised by the lamps and heating mat. This increased the locomotory activities of the insects. The insects visited hot and cold trays although they spent more time on the former. The numbers were fairly constant on the latter; they were also low on the hot tray

during mornng hours when the sand was perhaps not sufficiently hot. When the sand started heating, more insects were seen on it. This might be due to the fact that hot sand provided suitable basking sites. After 4 p.m. the frequency of visits to hot sand gradually decreased with an increase in visits to grass, possibly for feeding or resting. The percentage frequency of grasshopper-hours spent on hot and cold sand and on grass (Table 7) suggests that the two species spend almost

Table 7. *Time spent by* C. parallelus *and* C. brunneus *in different places in the cage*

Figures in grasshopper-hours

	C. parallelus	*C. brunneus*
Cold sand	17 (5)	26 (11)
Hot sand	91 (26)	64 (18)
Grass	154 (44)	151 (43)
Board	87 (25)	97 (28)
Totals	349 (100)	348 (100)

the same fractions of their time on sand (hot and cold together), board, and grass. The time spent on hot and cold sands was in the ratios 1·8 : 1 in *C. brunneus* and 5·2 : 1 in *C. parallelus*.

The percentage frequency of pods laid in warm and cold sand is shown in Table 8. Both species laid about 70% of their pods in the hot sand and 30% in

Table 8. *The number of egg-pods laid by* C. parallelus *and* C. brunneus

	Hot sand	Cold sand	Total egg-pods
C. parallelus	45 (68)	19 (32)	64
C. brunneus	59 (71)	28 (29)	87

cold, *i.e.* in the ratio 2·3 : 1. It appears, therefore, that *C. brunneus* spent more time on the hot sand almost in the same proportion as it laid in it, and in this species basking might be the reason for choice of oviposition site though it was not proved. In *C. parallelus* the proportions are (hot : cold sand) 91 : 17 for sitting and 45 : 91 for pods. The value of χ^2 is about 4·72 ($0{\cdot}5 > P > 0{\cdot}2$). In this species it looks as if the extra time spent basking on the hot sand did not lead to an equivalent excess of pods. Perhaps, therefore, in this species basking is more important than oviposition in the choice of warm sand. This might be because this species prefers moist sand and the warm sand may well be rather dry.

FACTORIAL EXPERIMENTS

After studying the effects of moisture content, particle size and compaction one at a time, their combined influence on the selection of oviposition sites was studied. Although the temperature of sand has an important influence it could not be studied in conjunction with other factors on account of the experimental difficulties. Experiments considering the pairs of factors moisture content with compaction and moisture content with particle size were studied, but since the testing of data by statistical methods did not reveal any significant results, these two experiments are omitted.

In this experiment three factors, moisture content, compaction and particle size of sand, were studied together. All these factors were considered at two levels. The following treatments were prepared: fine loose, fine compact, coarse loose,

Table 9. *The number of egg-pods laid by* C. parallelus *and* C. brunneus

	Dry				Wet				Total
	fine loose	fine compact	coarse loose	course compact	fine loose	fine compact	coarse loose	coarse compact	egg-pods
C. parallelus	0	1	3	3	1	2	7	0	
	0	0	2	1	2	2	6	3	
	0	1	2	2	1	2	9	3	
	1	2	3	2	1	0	4	4	
	1	4	10	8	5	6	25	10	69
C. brunneus	8	9	4	2	6	16	4	5	
	5	2	3	0	2	8	1	4	
	11	10	8	1	4	6	2	5	
	8	8	6	8	3	11	1	6	
	32	29	21	11	15	41	8	20	177

and coarse compact all made up in dry sand with no water added, and the same four made up in wet sand (20 ml of water added). Four replicates of each treatment were placed in two separate cages at random. The experiment was carried out with thirty gravid females of *C. parallelus* and *C. brunneus* in separate cages kept under identical conditions in a constant temperature room (30° C and R.H. 65%).

The analysis of variance was applied to the data summarized in Table 9 to examine the relative importance of the main factors and their interactions. The full analysis is shown in Table 10 and the following conclusions may be drawn:

Table 10. *Analysis of variance applied to square root transformations of the data summarized in Table 9*

Source of variance	Degrees of freedom	Sum of squares	Mean square	Variance ratio
Species (s)	1	364·500	364·500	64.71***
Moisture content (m)	1	6·125	6·125	1·09 n.s.
Texture (t)	1	12·500	12·500	2·22 n.s.
Compaction (c)	1	4·500	4·500	1
s × m	1	32·000	32·000	5·69*
s × t	1	276·125	276·125	49·09***
s × c	1	45·125	45·125	8·02*
c × t	1	55·125	55·125	9·08**
c × m	1	40·500	40·500	7·20*
m × t	1	4·500	4·500	1
m × t × s	1	3·125	3·125	1
m × t × c	1	10·125	10·125	1·80 n.s.
t × c × s	1	0·500	0·500	1
m × c × s	1	136·125	136·125	24·20***
t × c × s × m	1	0·000	0·000	1
Residue	16	90·000	5·625	
Total	31	1081·875		

* significant at the 5% probability level
** significant at the 1% probability level
*** significant at the 0·1% probability level
n.s. not significant

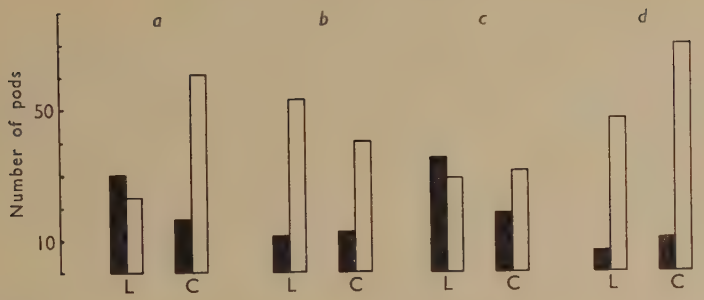

Fig. 5. Tue oviposition preference of *Chorthippus* in different treatments of sand. *a*, wet, *b*, dry, *c*, coarse, *d*, fine, L, loose, C, compact. ■, *C. parallelus*, □, *C. brunnues*.

1. *C. brunneus* laid more egg-pods than *C. parallelus*.

2. The other main factors, moisture content, particle size and compaction, had no significant effect although some of their interactions are significant.

3. *C. parallelus* showed a preference for moist sand and *C. brunneus* for dry sand (Fig. 5*a* and *b*).

4. The value of *F* calculated for the species-particle size interaction is significant. *C. parallelus* laid more egg-pods in coarse sand, while *C. brunneus* preferred fine sand.

5. *C. brunneus* laid more egg-pods in compact sand and *C. parallelus* in loose sand (Fig. 5*c* and *d*).

6. Both species prefer to oviposit in loose soil if it is coarse (Fig. 5*c*) but not if the sand is fine and compact.

7. When moist sand is offered for egg-laying both species prefer to lay eggs in compact sand. If the sand is dry, they prefer to deposit their egg-pods in loose sand.

8. *C. parallelus* prefers loose, wet sand while *C. brunneus* prefers compact, wet sand. Preference of the latter for compact wet sand is stronger than that of *C. parallelus* for loose wet sand (Fig. 5*a*). *C. brunneus* laid nearly four times as many egg-pods as *C. parallelus* in dry loose and dry compact sand (Fig. 5*b*).

DISCUSSION

Previous observations on the oviposition habits of grasshoppers and locusts suggest that most of the acridids have restricted oviposition sites the selection of which varies from species to species. Experiments with *C. parallelus* and *C. brunneus* show that the moisture content of the soil has a significant effect on the choice of oviposition site. The former prefers moist sand for egg deposition, and that is probably why the species is widely distributed in damp meadows and pastures. *C. brunneus* occurs commonly in sandy heaths and such dry habitats

as it prefers to lay in dry and hard sand. The soil structure and texture are also of considerable importance. The combined effects of soil compaction, texture and moisture contents have been stated earlier. These results provide explanations for the selection of light and soft soil, bare patches and anthills in fields as suitable egg-laying sites. On the basis of morphological characters of their ovipositors Agarwala (1953) has suggested that these two species are associated with loose soil, but his statement for *C. brunneus* does not agree with my observations. Waloff (1950) classified them as mesophilous insects on the ecology of their egg-laying habits.

That soil reaction might also influence the gravid females in the selection of oviposition sites was suggested by Professor G. J. Spencer (private communication), who has observed that *Camnula pellucida* (Scudder) on the Chilcotin Plateau, British Columbia, deposits eggs in soil of pH 7 - 8·4, although the preference does not hold good for the same species in California, where it lays in soil down to pH 6·5. No such association could be found in the present investigation. The distribution of British grasshoppers, especially *Chorthippus parallelus* and *C. brunneus*, is very wide; both are found on the chalk hills as well as on sandy heaths where the soil is slightly acidic.

The soil temperature has a significant effect on the choice of oviposition site. Criddle (1933) in his studies on the selection of egg-laying site by *Camnula pellucida*, *Melanoplus mexicanus mexicanus* (Saus.) and *M. packardi* Scud., has observed that during the early part of the egg-laying season, when the sun is hot and the soil warm, the level or eastern slopes are chosen, while in autumn the southern and western slopes are favoured. In eastern Siberia, the ovipositon of *Chorthippus albomarginatus* (De Geer) (Rubtzov 1935) took place mainly when the soil temperature varied between 31 and 33° C, was reduced when it was between 22 and 31° C and again when it rose to 34-35° C. Znamenskii (1951) and Choudhuri (1956*b*) have also shown that the soil temperature has some influence on oviposition site in *Locusta migratoria migratorioides* (R. & F.). Both *Chorthippus parallelus* and *C. brunneus* laid a large number of pods between 28 and 35° C. Their preference for warm sand may explain why bare patches, anthills or earthen mounds in habitats with otherwise dense vegetation are usually chosen for egg-laying. Also these places are warmer than grass-covered soil and offer suitable basking sites.

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SUMMARY

1. The effect of moisture-content, soil structure, particle-size, soil-reaction and soil temperature on the choice of oviposition sites in *Chorthippus parallelus* and *C. brunneus* were studied experimentally.

2. *C. parallelus* shows a distinct preference for moist sand while *C. brunneus* prefers dry sand for oviposition.

3. A tendency to dig more trial holes in sand with increasing moisture content was shown by both species, especially by *C. brunneus*.

4. *C. brunneus*, but not *C. parallelus*, prefers compact sand for oviposition.

5. *C. parallelus* prefers coarse and *C. brunneus* medium and fine sand.

6. The combined influence of moisture-content, compaction and particle-size of sand has a significant effect on the choice of oviposition site.

7. The two species studied do not show any marked oviposition response to the soil-reaction.

8. The temperature of soil has a pronounced effect on the choice of oviposition site in both species.

9. It is most likely that in *C. parallelus* basking is more important than oviposition in choice of warm sand.

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THE PSOCID FAUNA OF LARCH TREES IN NORTHERN ENGLAND—AN ECOLOGICAL STUDY OF MIXED SPECIES POPULATIONS EXPLOITING A COMMON RESOURCE

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(With 5 Figures in the Text)

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INTRODUCTION

The plants growing on the bark of trees lichens, algae and fungi—support populations of a number of different kinds of animals. By far the most important of these in northern England, both as regards numbers of individuals and biomass, are the psocids or barklice. In larch plantations in the Pennine hills and their foothills, a number of these psocid species live together. The question therefore arises whether these species are making common demands on environmental resources and, if so whether any of these resources are sometimes in short supply. Should this occur, these species populations will be competing both *inter se* and *intra se*, and the further problem arises whether these mixed populations maintain themselves as such permanently, or whether this competition results in local extinctions followed by local re-establishment by immigration. This paper deals with the food requirements of these psocid species, their distribution and density in the Pennine region, and the pattern of distribution in the heterogeneous environment of a single larch plantation.

FOOD AND FEEDING PREFERENCES

Psocids are pre-eminently insects of woodland and forest communities in Britain and are to be found on all kinds of trees. Only a few species occur in other habitats in this country. The adults, for the most part fully winged, are about 3-6 mm long and may be recognized in the field by the roofwise disposition of the wings over the abdomen and the fairly long antennae. Most of the common species present on larch in northern England have only one generation a year and overwinter in the egg stage. The eggs are in all cases laid on the bark, and the nymphs are miniature adults except for the small developing wings and genitalia. Both nymphs and adults spin silk, the amount varying considerably according to the species. Of the twenty-four psocid species occurring on larch trees in the Pennine region, the nine species, which together make up 95% of the total psocid population (Tables 5 and 6), are the ones most important ecologically from the point of view of grazing pressure on the food supplies. The investigation of feeding preferences and of the food taken in the field has been limited to these nine species. These are *Philotarsus picicornis* (F.), *Reuterella helvimacula* (End.), *Elipsocus westwoodi* McL., *E. mclachlani* Kimmins, *E. hyalinus* (Steph.), *Amphigerontia bifasciata* (Latr.), *A. contaminata* (Steph.), *Mesopsocus immunis* (Steph.) and *M. unipunctatus* (Müll.).

At all the localities studied, living and dead larch branches provide different microhabitats for psocids. At the highest localities, above 1000 ft above sea level, this difference is the most striking. The dead branches here are covered almost entirely by the lichen, *Lecanora conizaeoides* Cromb., little or no *Pleurococcus* being present. Lichen is also present on the thicker basal portions of the living branches, but the younger and thinner portions carry appreciable quantities of *Pleurococcus* and fungal spores with only little or no lichen. The different composition of the psocid fauna on the living and on the dead branches, illustrated in a general way by the total captures over the whole region, in Tables 5 and 6, suggests that some species may be lichen feeders and others may be living chiefly on *Pleurococcus* and fungal spores. The feeding habits of the nine commonest species have been investigated:

(*a*) by means of laboratory preference experiments, the animals being offered the choice of *Pleurococcus* and lichen;

(*b*) by grazing experiments, in which individuals of each species were enclosed on lichen alone and others on *Pleurococcus* alone;

(*c*) by measuring the oviposition rates of four selected species, when fed on *Pleurococcus* on the one hand and on lichen on the other;

(*d*) by examination of the gut contents of individuals captured in the field.

(*a*) *Preference experiments*

In these experiments, groups of individuals were given the choice of abundant *Pleurococcus* and abundant lichen for a period of about 3 days, at the end of which

time the distributions of the individuals themselves and of the faeces and eggs were recorded. Composite twigs were made by joining end to end a 10 cm length of dead larch twig covered completely on its upper surface with *Pleurococcus*, to a similar length completely covered above with lichen. These twigs were all about 5 mm in diameter, and were all obtained from the same source. The former were collected from a plantation at Harrogate. They carried a certain amount of dark brown detritus on the under-surface and the upper side was covered uniformly with a thick bright green layer of *Pleurococcus*, many cells deep. Microscopic examination indicated the presence of an almost pure culture of this alga, very few fungal spores and no lichen being present. The lichen-covered twigs were all obtained from the Ha Mire plantation at Malham Tarn. On the under-side of these twigs the bark was covered with a very thin compact layer of black detritus, and the upper surface was completely covered with a thick layer of the lichen, *Lecanora conizaeoides*, about 2 mm thick, no *Pleurococcus* being present. Fresh twigs were used for each experiment. The composite twigs were supported at each end on inverted pins pushed through corks, and were accommodated in pairs in covered circular glass tanks 25 cm in diameter at almost 100% R.H., with the twigs at right angles to the diffused light from a screened window. The laboratory temperature was 16-23° C. Nine to fourteen 5th-6th instar nymphs (five in the case of the *Mesopsocus* species) were placed uniformly along each composite twig and at least four such twigs were set up for each of the nine species. After 3 days, the number of nymphs on each half of the composite twig and the number of faeces underneath each half were recorded. The extent of the grazing was also noted. The amount of food consumed during the 3-day period was always less than one-third of the food available, so that in no case did a shortage of the preferred food affect the distribution of the individuals at the end of the experiment. In several of these experiments the gut contents of individuals present on each half of the twig and the faeces were examined microscopically.

The whole series of experiments was repeated using adult females, in place of nymphs, of each of the nine species in turn. Again at least four replicates were set up for each species. The twigs were first cleared of eggs, and the number of eggs laid during the 3-day period on each half of the composite twigs was recorded, as well as the distribution of adults and of faeces.

The small numbers of nymphs and adults that dropped off the twigs during these experiments were discarded. Faecal counts were not possible in the case of *Reuterella*, because it spins silken tents, under which the individuals spend most of their time and under which the faeces are deposited. A small proportion of the faeces of *Philotarsus* adhered to the appreciable quantity of silk produced by both nymphs and adults, but virtually all the faeces produced by the other species fell from the twigs on to the floor of the container. Adults and nymphs of these species produce only a little silk on the surface of the bark.

Since individual nymphs of *Amphigerontia* cannot be determined to species with certainty, the *A. bifasciata* nymphs were collected from a locality (Thruscross) where sampling the previous year had shown this species to be common and *A.*

contaminata very rare. The thirty-six nymphs used in the experiments were bred out, thirty adults being obtained of which twenty-nine were *A. bifasciata* and only one *A. contaminata*. The *A. contaminata* nymphs were taken from a batch collected at Aberford, the remaining nymphs being bred out, yielding forty-four adults, all of this species.

Table 1. *Preference experiments with nymphs*

	Number of nymphs per composite twig	Number of composite twigs	Number of nymphs		Number of faeces	
			on *Pleurococcus*-covered half	on lichen-covered half	under *Pleurococcus*-covered half	under lichen-covered half
Mesoposocus immunis	5	4	14	4	1699	359
M. unipunctatus	5	4	17	0	1742	221
Amphigerontia bifasciata	9	4	34	2	3563	287
A. contaminata	9	4	30	4	3691	1441
Philotarsus picicornis	10	4	36	2	3431	448
Elipsocus westwoodi	12	8	62	22	6264	2050
E. hyalinus	12	4	29	8	1043	658
E. mclachlani	10	4	9	28	557	2222
Reuterella helvimacula	14	8	23	84	–	–

The resulting distributions of the individuals themselves and of the faeces and eggs after 3 days are recorded in Tables 1 and 2, in which the figures for each species represent the summed counts from all the replicates. Replication over the four or more composite twigs was good for both nymphs and adults of all species, except for nymphal *Elipsocus hyalinus* and for the egg distribution of *Reuterella*, where twenty-four of the thirty eggs recorded on *Pleurococcus* were laid on one of the composite twigs by two females. Seven of the nine species clearly prefer *Pleurococcus* whereas the two remaining species, *Elipsocus mclachlani* and *Reuterella helvimacula*, prefer lichen, when both foods are present in abundance. These distributions must be regarded as the resultant of the action of two antagonistic factors. On the one hand, the preference shown by the animals for one food will tend to aggregate them on to one half of the composite twig. The relatively high density on the other hand, will promote a spacing out of individuals over the entire twig and this effect will vary with the species, depending partly on the activity of the individuals and partly on their relative tolerance to the close proximity of others of their kind. This is illustrated for the two *Mesopsocus* species in Table 3, where the distributions recorded in Table 1 are compared with those obtained with fifteen nymphs per composite twig instead of five. The counts from four replicate twigs for each species at each density are summed and expressed as ratios of the total number on the *Pleurococcus*-covered halves of the composite twigs to the total number on the lichen-covered halves at the end of the experiment. For each species, the ratios for both nymphs and faeces are smaller at the

higher density. Increase in density results in a greater spacing out of individuals over the whole twig, a greater proportion of the nymphs resting on the lichen-covered half. Also, at each density, the ratios for *Mesopsocus immunis* are smaller than those for *M. unipunctatus*, since individuals of the former species space themselves out over the whole twig to a greater extent than those of the latter.

Table 2. *Preference experiments with adult females*

	Number of females per twig	Number of composite twigs	Number of females on *Pleurococcus*-covered half	Number of females on lichen-covered half	Number of faeces under *Pleurococcus*-covered half	Number of faeces under lichen-covered half	Number of eggs (or egg batches) on *Pleurococcus*-covered half	Number of eggs (or egg batches) on lichen-covered half
Mesopsocus immunis	5	8	28	10	2509	603	15	26
M. unipunctatus	5	8	22	10	2825	436	23	16
Amphigerontia bifasciata	6	4	22	0	3260	280	318	100
A. contaminata	7	4	21	6	5619	466	522	45
Philotarsus picicornis	10	4	36	3	5423	237	457	54
Elipsocus westwoodi	10	4	35	1	3927	436	309	128
E. hyalinus	10	4	32	6	3367	1494	216	143
E. mclachlani	12	4	16	27	959	3292	94	388
Reuterella helvimacula	10	4	4	28	–	–	30	156

Since an examination of gut contents at the end of the experiment showed that no lichen had been taken by either species even at the higher density, this difference must be ascribed to *M. immunis* being less tolerant of the close proximity of others of its kind than is *M. unipunctatus*. For this reason the figures recorded in Tables 1 and 2 cannot be used in any simple way as an index of the degree of preference for one or other of these foods. *Elipsocus mclachlani* and *Reuterella helvimacula* are the species most tolerant of high densities, since they are the only two of these species in which individuals tend to form clusters. These and the nymphs of the

Table 3. *Preference experiments with* Mesopsocus *at two population densities*

Figures show the ratios of the numbers on *Pleurococcus*-covered halves to the numbers on lichen-covered halves of composite twigs.

Density (numbers per composite twig)	*M. immunis*		*M. unipunctatus*	
	nymphs	faeces	nymphs	faeces
15	1·9	1·5	2·2	4·3
5	3·5	4·7	17·0	7·9

two *Amphigerontia* species are the least active. Somewhat more active are *Philotarsus picicornis*, *Elipsocus westwoodi* and *E. hyalinus* but the most agile are the nymphs and adults of the two *Mesopsocus* species which are more sensitive to disturbance than the others and which can run about on the twigs very rapidly indeed. Some allowance for these differences between the species and for size

differences as well were made in the experiments by using smaller numbers of individuals per composite twig for the two *Mesopsocus* species and for the adults of the two species of *Amphigerontia*.

The observations on the extent of grazing and the microscopic examination of gut contents and faeces at the end of the experiments give a clear indication of the food eaten and so provide valuable data for the interpretation of the results tabulated, which in themselves merely provide an index of the relative time spent on the two portions of the composite twigs. In the case of *Mesopsocus immunis*, *M. unipunctatus*, *Philotarsus picicornis* and *Elipsocus westwoodi*, the *Pleurococcus* had been noticeably grazed, but only an occasional fructifying cup of the lichen had been nibbled. The gut contents of individuals, even of those resting on the lichen at the end of the experiment, consisted almost entirely of *Pleurococcus* cells, together with small amounts of bark and detritus particles. The faeces under the lichen-covered half of the composite twigs also showed this same composition. These species, then, both as nymphs and as adults, avoid lichen entirely when *Pleurococcus* is readily available to them. This is true also of the *Amphigerontia* species, both of which nibbled only the occasional fructifying cup of the lichen. These two species, however, did show a difference, which may well produce a difference in the response of natural populations to a shortage of *Pleurococcus*. In the case of *Amphigerontia bifasciata*, the faeces under both halves of the composite twigs were of the same composition, consisting of *Pleurococcus* cells with small quantities of bark and detritus. The animals had fed upon the *Pleurococcus* but had evidently moved about freely, some of them depositing their faeces from the lichen-covered half of the twig. The faeces of *Amphigerontia contaminata*, on the other hand, showed a marked difference in composition under the two portions of the composite twig. Under the *Pleurococcus*-covered half, the faeces were composed chiefly of *Pleurococcus* cells with some bark and detritus, whereas those beneath the lichen were made up almost entirely of bark and detritus. The gut contents of individuals, both nymphs and adults, on the two portions of the composite twigs at the end of the experiment showed the same difference in composition. Evidently *Amphigerontia contaminata* moves about in search of its preferred food less readily than *A. bifasciata*, and, perhaps as a result of this, it more readily takes detritus when *Pleurococcus* is not available in the immediate surroundings. Although the figures for *Elipsocus hyalinus* appear to indicate a weaker preference for *Pleurococcus* than the species so far considered, gut content and faecal examination showed that this species avoided lichen. The faeces were very similar under both halves of the composite twigs and consisted of *Pleurococcus* cells with sometimes a large amount of bark and detritus. The high faecal count under lichen was due, therefore, to the animals moving about fairly freely and to some grazing of the detritus on the underside of the lichen-covered half of the twigs. Lichen was taken occasionally, however. A small patch of lichen thallus had been grazed by one of the nymphs and the crop of one of the adults was full of lichen. The majority of the individuals on the lichen-covered half of the twigs at the end of the experiment had been eating either *Pleurococcus* or bark and detritus. *Elipsocus hyalinus* will therefore

very occasionally take lichen, even when *Pleurococcus* is abundant, but a clear preference for *Pleurococcus* is nevertheless indicated.

The remaining two species provide a sharp contrast to the seven species so far considered. Both *Elipsocus mclachlani* and *Reuterella helvimacula* show a marked preference for lichen. *Pleurococcus*, however, was noticeably grazed in the small areas where a cluster of individuals had formed, and the gut contents of these individuals at the end of the experiment consisted almost entirely of *Pleurococcus* cells with only small amounts of bark and detritus particles. The gut contents of individuals on the lichen-covered half of the twigs, on the other hand, consisted almost entirely of lichen with again small amounts of bark and detritus. These remarks apply both to the nymphs and to the adults of these two species. *Reuterella helvimacula* constructs silken tents over the axils of the short side shoots and most of the initial grazing had been done within these tents, where both the thallus and the fructifying cups had been grazed. The individuals of *Elipsocus mclachlani* had grazed the fructifying cups, eighty-eight of these having been grazed over the four experimental twigs by thirty-seven nymphs in 3 days, and 253 cups (about two-thirds of the total present) by forty-three adult females in the same period. None of the thallus was taken.

The egg distributions in all, except *Mesopsocus immunis*, follow broadly the distributions of the individuals and of the faeces. Any discrepancy in detail between egg distribution and the distribution of individuals and faeces is likely to be due to the effect of the high density of feeding individuals on one half of the composite twig interfering with oviposition under the particular conditions of these experiments. This probably accounts for the reversed egg distribution of *M. immunis* when compared with *M. unipunctatus*, since *M. immunis* has been shown to be less tolerant of high population densities than *M. unipunctatus*. It may be said, then, that these nine species all tend to oviposit where they are spending most of their time. Under the conditions of these experiments, the animals spend most time on that portion of the composite twig, where their preferred food is most abundant. It will be seen later that the correspondence between the distribution of individuals (and therefore presumably also of the eggs) and the distribution of the food is not always a close one under natural conditions.

These experiments indicate that, with both *Pleurococcus* and lichen available in abundance, seven of the nine commonest psocid species on larch take *Pleurococcus* and reject the lichen almost completely, whereas the other two species prefer lichen, but will feed on *Pleurococcus* as well quite readily. Also, since nymphs and adults do not differ in this respect, and since adults lay their eggs where they spend most of their time, the effective habitat in nature, in the case of each of these species, will be the same for all stages of the life history.

(*b*) *Grazing experiments*

The preference experiments described above gave information on the relative amounts of *Pleurococcus* and lichen eaten when both were present in abundance.

The following experiments were designed to find out how readily these species will take the alternative food when their preferred food is not available. For each species a group of individuals was enclosed in a 3×1 in. tube at 100% R.H. on a 7 cm length of dead larch twig carrying *Pleurococcus*, and another group of the same number, picked out at random from the same collection, was enclosed on a similar length of dead larch twig carrying lichen only. These twigs were identical to those used in the preference experiments, the upper surface of the twig being completely covered with either *Pleurococcus* or lichen and the under surface carrying a thin layer of brown or black detritus. When all the food in one of the tubes was exhausted, observations were made on the type and extent of grazing on both twigs, on the number and general condition of the survivors, and, where desirable, on the composition of the faeces and gut contents.

The results of the experiment with *Amphigerontia bifasciata* will be described in detail, as being typical of the seven *Pleurococcus*-preferring species. Eleven female *Amphigerontia bifasciata* were enclosed on a 7 cm length of *Pleurococcus*-covered twig and eleven more were enclosed on a lichen-covered twig for 6 days. After this period of time almost all the *Pleurococcus* had been grazed away, and the underside of the twig was cleared of the small amount of detritus present. The faeces in this tube were composed almost wholly of *Pleurococcus* cells with small amounts of bark and detritus particles, and the gut contents of the individuals on this twig were of the same composition as the faeces. Ten females were still alive after 6 days and twelve egg clusters had been laid. On the lichen-covered twig the lichen thallus was untouched and only twelve fructifying cups had been nibbled, but the underside of the twig, previously black in colour owing to the presence of a very thin layer of detritus, had been grazed down completely to the pale brown bark. The gut contents of the surviving individuals and the faeces were composed almost entirely of bark flakes and black detritus particles, but with a small proportion of lichen gonidia and hyphal material. The faeces in this tube numbered only about one-tenth of those in the tube containing the *Pleurococcus*-covered twig. Only five individuals were alive at the end of the experiment and only one egg cluster had been laid. It is clearly evident from these observations that *Amphigerontia bifasciata*, when presented with lichen alone, gradually starves to death. Any detritus on the twig is preferentially taken, but this appears to be very much less nutritious than *Pleurococcus*. These remarks apply, in all essential points, to the other six *Pleurococcus*-preferring species. It is also worthy of note that, in both the preference and the grazing experiments, the small amounts of lichen taken by these species almost invariably comprised the fructifying cups only. These are evidently slightly less unpalatable than the thallus of the lichen. Evidence will be presented later to show that these fructifying cups are the only portions of the lichen free from lichen acid.

The two lichenophilous species will be considered separately. In the case of *Reuterella helvimacula* forty females were placed on the *Pleurococcus*-covered twig and another forty on the lichen-covered twig. After 8 days, none had died on either twig. The *Pleurococcus* was grazed away almost completely and the individuals on this twig

were all in good condition, with their crops full of algal cells. Moreover, little or none of the detritus on the under surface had been removed, so that *Pleurococcus* is taken in preference to detritus in these circumstances. The whole surface of the lichen, apothecia and thallus alike, had been grazed, about half of it superficially revealing the bright green algal layer of the thallus, and the other half more deeply revealing the white fungal medulla below. The gut contents of the individuals on this twig consisted of lichen gonidia and macerated hyphae. Thus, although *Reuterella* shows a preference for lichen when this and *Pleurococcus* are presented to it together, it nevertheless accepts *Pleurococcus* as readily as lichen when these foods are presented to it separately. The results of the experiment with *Elipsocus mclachlani*, in which twenty females were placed on each kind of twig for 14 days are similar to those with *Reuterella*, in so far as the *Pleurococcus* was taken as readily as the lichen. Almost all the *Pleurococcus*, but none of the detritus, had been removed, and ninety-eight fructifying cups of the lichen were grazed, representing over two-thirds of the apothecia present. The other observations on *Elipsocus mclachlani*, however, were unexpected. About four times as many faeces were produced on *Pleurococcus* as on lichen. There were eight survivors on the *Pleurococcus* on which 339 eggs had been laid, but no survivors on the lichen-covered twig on which only 186 eggs were counted. This difference is partly to be accounted for by the peculiar conditions of the experiment. The individuals congregated at the upper end of the vertically placed twig, where a local shortage of food developed and where the superficial grazing of the apothecia down to only the algal layer indicated considerable mutual interference with feeding and, no doubt, with oviposition as well. Although these particular results are therefore inconclusive, they do suggest that *Elipsocus mclachlani* can assimilate *Pleurococcus* more quickly than the lichen.

These grazing experiments indicate that, in the absence of *Pleurococcus*, the seven *Pleurococcus*-preferring species take only very small amounts of lichen, prefer detritus to lichen, and gradually starve to death. The two lichenophilous species, on the other hand, in the absence of lichen, eat *Pleurococcus* very readily, taking it in preference to detritus, and appear to thrive on it.

(*c*) *Oviposition rates*

The difference between the *Pleurococcus*-feeding and the lichen-feeding species, with regard to the utilization of the less preferred of these two foods when the preferred one is not available, has been examined in more detail by measuring the oviposition-rates of individuals fed on *Pleurococcus* alone and of others fed on lichen alone. The eggs of all these psocids are relatively large and yolky, and oviposition-rates are high under favourable conditions. In the preference experiments, for instance, the oviposition-rate of *Philotarsus picicornis* averaged 4·3 eggs per female per day. Since this requires a considerable and rapid mobilization of protein, oviposition-rate would be expected to be a sensitive index of nutritional level. Under conditions of food shortage in nature this will depend upon many factors, among which the time spent in searching for food and the readiness with

which less preferred foods are taken, together with their nutritive value, will be the most important. Under such conditions a reduction in oviposition-rate may well be the most important factor initially in determining future population trends.

Four species only were chosen for study: the two lichen-preferring species *Reuterella helvimacula* and *Elipsocus mclachlani*, *E. westwoodi* as a typical *Pleurococcus*-preferring species, and *Elipsocus hyalinus*, since the preference experiments yielded less decisive information on this species than on the others. For each species, ten groups of freshly caught adult females of mixed ages were placed separately on five *Pleurococcus*-covered and five lichen-covered dead larch twigs. Each twig with its group of females was housed in an inverted 3×1 in. glass tube with a perforated cork covered with bolting silk as a stopper, and the tubes were kept in a desiccator jar at 100% R.H. at room temperature, 19° to 23° C. The number of females per twig varied with the species, being six in *Elipsocus mclachlani* and in *E. hyalinus*, seven in *E. westwoodi* and ten females per twig in the case of *Reuterella*. The twigs were each 7 cm long and about 5 mm in diameter, and were uniformly and completely covered on their upper surface with *Pleurococcus* or with fructifying lichen. Small amounts of brown or black detritus were present on the lower surface of both kinds of twig. Any eggs present on them were removed and the twigs were then conditioned at 100% R.H. for 24 h before use. In order to assess the nutritional value of the detritus five additional twigs, lichen covered but with all the detritus scraped away from the lower surface, were set up, each with six female *Elipsocus hyalinus*, since it was known that this species takes detritus in preference to lichen if no other food is available. Each group of animals was transferred to a fresh twig at the end of 2 days and the number of eggs laid and the number of females dying during the 2-day period were recorded. This was repeated for 3 more consecutive 2-day periods so that four such recordings were obtained for the 8-day period of each experiment. In this way an abundant supply of fresh food was assured during the whole period, and an accumulation of eggs which might have resulted in egg eating was avoided. In no case was there any indication of eggs' having been eaten.

The average number of eggs laid per female and the total number of individuals surviving, for the four consecutive 2-day periods, on the *Pleurococcus*-covered and on the lichen-covered twigs are represented graphically in Fig. 1. The females of the parthenogenetic species *Elipsocus hyalinus* were relatively young, as indicated by the very low mortality on the *Pleurococcus*-covered twigs, and they did not reach their peak oviposition until the fourth day of the experiment. Since the other three species are bisexual, older individuals with fat abdomens were chosen in order to ensure that only fertilized females were used. The progressively smaller number of eggs laid therefore reflects the ageing of the individuals. Since the females were apportioned at random on to the two kinds of twigs, the slope of the oviposition curves may be disregarded.

Comparison of the oviposition and survival curves for *Pleurococcus* with those for lichen shows that the four species fall into two distinct groups, the two *Pleurococcus*-preferring species, *Elipsocus hyalinus* and *E. westwoodi*, on the one

hand and the two lichen-preferring species, *Reuterella helvimacula* and *Elipsocus mclachlani*, on the other. In both of the *Pleurococcus*-preferring species the oviposition-rate on *Pleurococcus* was much greater than that on lichen, and the mortality-rate was much less. *Pleurococcus* is probably an adequate food for these two species but lichen is clearly unsuitable for them. It may be both unpalatable and indigestible but these cannot be separately assessed from the results of these experiments. The fact that the oviposition- and mortality-rates of *Elipsocus hyalinus* were the same for the lichen-covered twigs with and without detritus, suggests that detritus has little or no nutritive value, so that the oviposition of this species and

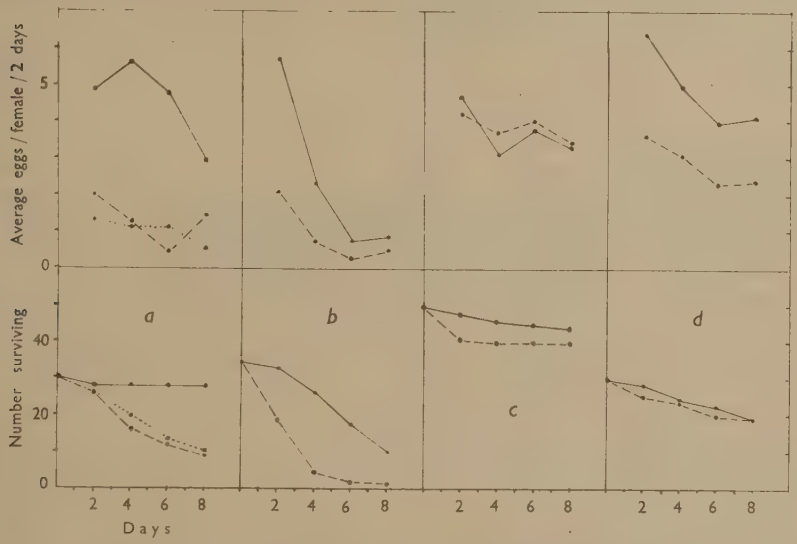

Fig. 1. Oviposition- and survival-rates of four psocid species; ●—●, on *Pleurococcus*; ● — — —●, on lichen; ●.....●, on lichen (detritus on underside of twig removed).
a, Elipsocus hyalinus; *b, E. westwoodi*;
c, Reuterella helvimacula; *d, Elipsocus mclachlani*.

also of *E. westwoodi* on the lichen-covered twigs is probably due entirely to the ingestion of lichen. Both of the lichenophilous species show no significant difference between their mortality-rates on the two foods, and the oviposition-rate is as high on *Pleurococcus* as it is on lichen. In the case of *Reuterella* oviposition-rates on the two foods are the same, suggesting that populations of this species will not suffer reduction during shortages of their preferred food, provided that *Pleurococcus* is available to them in adequate amounts. *Elipsocus mclachlani*, however, is highly peculiar in that its oviposition-rate on *Pleurococcus* is almost twice as great as that on its preferred food, lichen. This confirms the tentative conclusions arrived at from the grazing experiments already described, and is not subject to the same difficulties of interpretation as the latter, since the frequent provision of fresh food and the use of only a small number of females on each twig ensured that there was never a shortage of food. The preference shown by *Elipsocus mclachlani* for

lichen, when both this food and *Pleurococcus* are available in abundance, and also the similarity in the mortality-rates on these two foods in these oviposition experiments, both indicate that this species is adapted to lichen feeding. This difference between the oviposition-rates on *Pleurococcus* and on lichen does, however, suggest that this species can digest and assimilate *Pleurococcus* more quickly than it can the apothecia of the lichen on which it habitually feeds. In this respect it must be regarded as incompletely adapted to a lichen diet.

(*d*) *The natural grazing of* Elipsocus mclachlani *and* Reuterella helvimacula

Further evidence of the incomplete adaptation of *Elipsocus mclachlani* to a lichenophilous mode of life is provided by comparison of the grazing habits of this species with those of *Reuterella helvimacula*. Both the nymphs and the adults of *R. helvimacula* construct small silken sheets slung across the axils of the short

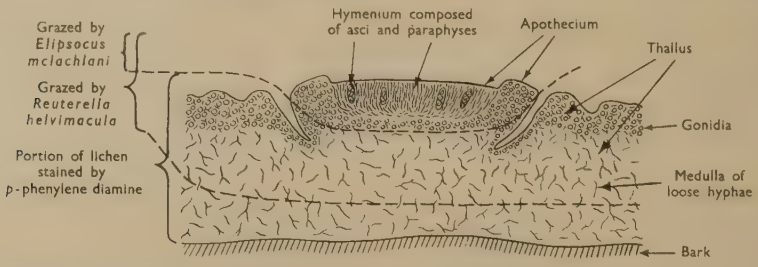

Fig. 2. Diagrammatic vertical section of the apothecium and thallus of the lichen, *Lecanora conizaeoides* Cromb.

lateral shoots on larch twigs. Within these tents, several individuals congregate and here they spend most of their time. The whole surface of the lichen within and around the tents is grazed first, and even at this early stage, when food is abundant and easily accessible, these animals exercise no discrimination between the apothecia and the thallus of the lichen. Later in the season, as the number of individuals increases, they graze the lichen at some distance from the web. On a thick larch branch 2 cm in diameter, observed at Fewston on 15 October 1955, the under-surface was completely covered by a continuous silken webbing, beneath which last instar nymphs about 1 mm long were present at an average density of 6 per sq. cm. The lichen covering the upper surface of this branch was completely grazed away down to the white fungal medulla, the whole of the apothecia and the gonidial layer of the thallus having been eaten away. In contrast to this, *Elipsocus mclachlani* grazes the fructifying cups only. No indication was obtained either in the field or in the laboratory that this species ever grazes the thallus of the lichen. The hymenial layer of the apothecia and the gonidial layer immediately below it are eaten to expose the white fungal medulla.

This lichen, *Lecanora conizaeoides*, is illustrated diagrammatically in vertical section in Fig. 2. Among the compounds which produce a colour reaction when applied to the appropriate lichen and which are generally regarded as reacting

with the contained lichen acid to produce the dye, is *para*-phenylene diamine which stains this species of *Lecanora* a deep reddish brown. When a solution of this compound in 70% alcohol is poured over a thin vertical section of the living lichen, the reddish brown dye is immediately produced everywhere except in the apothecium, *i.e.* except in that portion of the lichen which is eaten by *Elipsocus mclachlani*. It would appear then that the lichen acid renders the thallus unpalatable to *E. mclachlani*, so that only the fructifying cups, which are free from this substance, are available to this species. *Reuterella*, on the other hand, is presumably unaffected by the presence of the lichen acid, since it does not discriminate between thallus and apothecium. The whole of the lichen is available to this species and, in this respect, it is more completely adapted to a lichen diet than is *Elipsocus mclachlani*.

(*e*) *Analyses of gut contents*

The relative amounts of the different types of food eaten in nature were estimated by examination of the gut contents of freshly captured individuals to compare the feeding responses of the eight species when the main food items are available to all of them in the same proportions, to compare the ways in which each species reacts to a shortage of its preferred food, and to compare the foods taken by three species at two widely separated localities.

The components of the food taken by these psocids in the field are lichen, fungal spores, *Pleurococcus*, bark and detritus. Lichen in the gut can be recognized by the spherical algal cells of various sizes, clustered together and invested with hyphal material. Such clusters are derived from the thallus of the lichen or from the edges and deeper portions of the fructifying cups. It is usually possible to see distinct hyphae in crop contents, but, on further digestion, their hyphal form is lost, and the clusters of algal cells then appear to be invested with a homogeneous material, which still, however, is stained by aniline blue. Lichen is also frequently represented in the gut by small masses of hyphal threads lying parallel to each other and containing the asci with their spores derived from the hymeneal portion of the fructifying cup. Probably all the lichen found in the crops of these psocids was *Lecanora conizaeoides*, since this is virtually the only lichen present on the larch trees in the plantations studied. The algal or gonidial part of this lichen is a species of *Trebouxia*. The next component of the food comprises fungal spores of various kinds. A large proportion of these spores belong to one polymorphic fungus, probably an effused form of *Sporodesmium scutellare* Berk. & Br. (Moniliales). Smaller spores, with thinner and paler brown cell walls and usually occurring singly rather than in clusters, are often very frequent, and other spore types occur in smaller numbers. These 'honey-dew moulds' are extremely abundant on the bark of living twigs infested with *Adelges*, where they sometimes occur in almost pure culture, although they are usually found intimately mixed with *Pleurococcus*. In such places the presence of yeasts may also be expected. In summer these fungi are represented on the bark of twigs almost entirely in the form of spores, only very few hyphae being present. Nearly all of the free-living algae, found both on the

twigs and in psocid crops, were *Pleurococcus*, easily recognizable by the clusters of two or four cells produced by division. Other algae present in only very small amounts included *Trebouxia*, the algal constituent of the lichen. The last two constituents of the food are bark flakes, in which the cellular structure is usually clearly recognizable, and structureless brown or black particles here referred to as detritus. It is unlikely that either of these has much nutritional value for a psocid. Fungal hyphae are sometimes present, however, in the grooves of bark flakes found in the crop. Other materials in the gut, including pollen grains and portions of cuticle, were found only occasionally, and even then in only very small amounts. In the gut of three individuals antennae and legs of *Adelges* were recognized. They were probably cast skins taken inadvertently in grazing the *Pleurococcus*. Their extreme scarcity in the gut compared with the great abundance of *Adelges* on the larches indicates that these psocids do not prey upon other living animals. The fungal spores, bark and detritus are not stained by aniline blue. The contents of algal and lichen gonidial cells stain intensely with this dye, whereas the lichen fungus, in both the undigested and semi-digested states, is stained pale blue. It is clear from the examination of both gut contents and faeces that lichen and *Pleurococcus* are digested by all these species. The lichen fungus loses its hyphal form and the contents of most of the lichen gonidia and *Pleurococcus* cells disappear, although some of them certainly escape complete digestion, since chlorophyll can be extracted from the faeces. Presumably the fungal spores are digested too, since well-fed individuals containing many eggs have been dissected and found to contain little but fungal spores in the gut.

At Thruscross on 8 August 1955 individuals of seven of the commonest species were obtained from the living twigs and also from the dead twigs of a small clump of larch trees. The specimens, dislodged on to a tray by beating the twigs, were immediately transferred to 70% alcohol. These living larch twigs carried appreciable quantities of *Pleurococcus* and fungal spores but very little lichen, whereas the dead twigs carried an almost complete cover of lichen with only a little *Pleurococcus* in places. In each of these microhabitats, the food available was approximately the same for all seven species. At Witton Fell on 28 August 1954 a more precise collecting technique was used, and four species were obtained from both living and dead branches of the same trees. Lengths of twig 25 cm long and about 5 mm in diameter were sleeved in a long test tube, the twig being then cut off and the tube corked. The psocids on these twigs were removed in the laboratory within two hours after collection and preserved in alcohol. These twigs were selected for greatest homogeneity of the bark flora. The living twigs were almost completely covered on their upper surface with a mixture of *Pleurococcus* and fungal spores but with only an occasional lichen nodule. The dead twigs were completely covered with a pure culture of the lichen. On most of these, there was no visible trace of *Pleurococcus*, but on others very small patches of the alga were present, never amounting to more than 1% of the total surface area of the twig. On each type of twig the food available was therefore almost exactly the same for all four species.

After storing the specimens for some months in 70% alcohol, the gut contents

could easily be removed in the form of a compacted mass. The specimens were dissected in 70% alcohol, the abdomen being cut off and its cuticle removed. After slitting and opening up the brittle walls of the crop it was nearly always possible to remove the contents in one piece. When this was not possible, the contents of the loop of the intestine were dissected out, but rectal material was avoided. The crop contents were then pipetted on to a microscope slide, the alcohol removed with blotting paper, and a drop of lactophenol mixed with a very dilute solution of aniline blue was added. The crop contents were broken up with a needle, and after staining for two or three minutes were mounted under a cover slip. These

Table 4. *The relative proportions of five food components in the crops of individuals from (upper figures) living and (lower figures) dead twigs of larch*

	Food				
	Lichen	Fungal spores	*Pleuro-coccus*	Bark	Detritus
Thruscross, 8 Aug. 1955					
Mesopsocus immunis	0	31	21	18	10
	21	17	7	19	16
M. unipunctatus	0	31	12	22	15
	15	13	8	20	24
Philotasus picicornis	0	39	23	7	11
	1	27	11	18	23
Amphigerontia bifasciata	0	40	19	12	9
	27	10	3	21	19
Elipsocus westwoodi	0	39	27	6	8
	10	22	6	20	22
E. hyalinus	16	32	12	6	14
	25	18	19	4	14
E. mclachlani	29	23	13	5	10
	72	0	1	0	7
Witton Fell, 28 Aug. 1954					
Philotarsus picicornis	0	42	27	4	7
	5	14	30	11	20
Amphigerontia bifasciata	0	43	27	3	7
	9	13	26	10	22
Elipsocus westwoodi	0	40	28	2	10
	8	11	38	6	17
Reuterella helvimacula	4	41	26	4	5
	65	1	1	3	10

preparations remained in good condition for many months. The crop contents of ten individuals of each species from each microhabitat were mounted. Eight units, assigned to the gut contents of each individual, were divided out according to the relative abundance of the various components. These units, summed for each group of ten individuals, are presented in Table 4.

The first five species recorded in Table 4, all of which have been shown to prefer *Pleurococcus*, were all feeding at Thruscross on the same foods in approximately the same proportions. On the living twigs, where their preferred food is abundant, they avoid the small amounts of lichen present; on the dead twigs, where their

preferred food is scarce, they take bark and detritus in greater quantity and also some lichen as well. *Elipsocus hyalinus* is similar to these five species except for the relatively large amount of lichen taken from the living twigs. It will be recalled that in the preference experiments this species occasionally took appreciable quantities of lichen even when *Pleurococcus* was readily available in abundance. It is evidently more inclined to take lichen than these five species, although like them it is primarily a feeder on *Pleurococcus* and fungal spores.

The seventh species in Table 4, *Elipsocus mclachlani*, presents a marked contrast to the other six. From the dead twigs, it takes lichen only, and, from the living twigs, appreciable quantities of *Pleurococcus* and fungal spores as well as lichen. Slight differences between species in Table 4 cannot reasonably be assigned to inherent differences in feeding preference, since sampling errors are involved as well as errors in the estimation of the proportions of different foods in the gut. Moreover the food available was not precisely the same in composition over all the twigs from which the specimens were collected. The collecting technique at Witton Fell reduces this latter source of variation to insignificant proportions, and the uniformity of the results here shows that the sampling error and the error involved in estimating the relative proportions of the various foods are indeed very small. At Witton Fell three species, *Philotarsus picicornis*, *Amphigerontia bifasciata* and *Elipsocus westwoodi*, were feeding in exactly the same way when all were present in the same homogeneous environment. Again, as at Thruscross, these animals had evidently searched actively for the small amounts of *Pleurococcus* and fungal spores present on the dead twigs and had avoided the lichen to a considerable extent, as indicated by comparison of the proportion of lichen to total food in the gut (about 10%) with that on the twigs (over 95%). The fact that fungal spores were taken in consistently greater amounts than *Pleurococcus* from the dead twigs at Thruscross, whereas the reverse holds true at Witton, suggests that these species do not discriminate between these two foods, nor would such discrimination be expected since they are nearly always present on twigs in an intimate mixture. *Reuterella helvimacula* at Witton Fell was behaving in a very similar manner to *Elipsocus mclachlani* at Thruscross. It was feeding almost entirely on lichen on the dead twigs, and on the living twigs where its preferred food, lichen, was almost absent, it was taking chiefly fungal spores and *Pleurococcus*, these being present in the crop in the same proportions as in the other three species. This lichenophilous species also evidently shows no preference between these two foods. The greater proportion of lichen in the gut of *Elipsocus mclachlani* from living twigs, compared with *Reuterella*, does not indicate any inherent difference between these two species. The living twigs beaten at Thruscross carried more lichen than the living twigs sampled at Witton, and this no doubt accounts for the difference in gut contents observed.

These results show good agreement with the results of the various laboratory experiments already described. From all of them, the following conclusions emerge. Six of the eight commonest species feed primarily on *Pleurococcus* and fungal spores. These are *Mesopsocus immunis*, *M. unipunctatus*, *Philotarsus picicornis*,

Amphigerontia bifasciata, *Elipsocus westwoodi* and *E. hyalinus*. None of these species appears to discriminate between *Pleurococcus* and fungal spores. When their preferred foods are scarce, these species will take some lichen, *Elipsocus hyalinus* probably more readily than the others, but since lichen is an unsatisfactory food for them, producing higher mortality- and lower oviposition-rates, it is to be expected that under such conditions their populations could not maintain themselves for long, especially in competition with the lichenophilous species. The remaining two species, *E. mclachlani* and *Reuterella helvimacula*, feed primarily on lichen. When this is scarce or absent, *Pleurococcus* and fungal spores are readily accepted, however, and since oviposition-rates do not then show any reduction and mortality-rates are unaffected, it may be expected that populations of these species could maintain themselves, for considerable periods at any rate, on these foods in areas where lichen is scarce or absent. How successfully they do so in nature in face of competition from the *Pleurococcus*-feeding species will be examined in a later section.

THE DISTRIBUTION AND ABUNDANCE OF PSOCIDS IN THE PENNINE REGION

The eastern slopes of the Pennine Hills in Yorkshire provide a climatic gradient particularly suitable for a study of the distribution and relative abundance of psocids, since a knowledge of the way in which these populations vary with altitude will provide a background against which the ecological situation in any one plantation may be assessed, and will give some indication of the extent to which climate in a general sense sets a limit to population size. Accordingly, a census of psocid populations on both living and dead branches has been made in plantations of European larch (*Larix decidua* Mill.) at twenty-four localities at various altitudes between 100 and 1300 feet above sea level. The samples, taken by beating the branches in a standardized way and collecting the individuals dislodged, gave population density indices which allow comparison at different altitudes and on these two portions of the tree. Since some species develop earlier in the season than others, this survey was carried out in two parts; early summer populations were studied by sampling from ten of these localities and the later summer populations by sampling from all twenty-four localities.

(*a*) *Census method*

The choice of localities was determined by the availability of immature stands of unbrashed larch about 30-40 years old, and by the desirability of avoiding the heavily polluted industrial region which extends along the foothills of the Pennines southwards from Leeds. These plantations are mapped in Fig. 3, in which they are referred to, for the most part, under the name of the nearest village. The majority are situated in an area of about 800 square miles to the north and north-west of Leeds. Those at Witton Fell, Bradfield and Malham Tarn are the highest plantations in this region of the Pennines, where very few woodlands of any size are to be found above about 1000 ft. Samples were taken by beating branches

3-9 ft above the ground with a walking stick in a standardized way, the insects falling on to a cloth tray held closely beneath, from which they were collected by means of a suction tube and then preserved in alcohol. Winged individuals are dislodged from the twigs and fall on to the tray as readily as nymphs and make no attempt to fly away. The amount of larch branch covered by the walking stick held diagonally across it and regarded as one unit was repeatedly struck to dislodge as many of the insects as possible. Ten such units comprised one sample in the early summer survey and twenty such units formed one sample in the later summer census. Samples were taken in pairs, one of each pair from the terminal portions of the living branches, usually at the edge of a group of trees, and the other from the dead branches of the same trees, usually just within the canopy. Successive pairs of samples were taken from widely separated points in order to reflect the variation in abundance of psocids within any one plantation. These collections were made only from healthy trees in fairly large continuous stands. Small isolated groups of trees and isolated larches among deciduous trees were avoided since these would not be expected to carry a representative fauna. The census of psocid populations in the early summer was carried out over a period of 9 days between 27 June and 5 July 1955, when the two *Mesopsocus* species which form the major part of the psocid fauna at this time, were represented entirely by late instar nymphs and adults. The more extensive later summer survey occupied a period of about 6 weeks between 8 August and 24 September 1954, when both nymphs and adults of all the common species were present on the twigs. Since adults emerge earlier in the warmer lowland localities than in those at higher altitudes, the majority of the former were sampled in the first half of the period between 8 and 21 August and most of the highland localities were sampled in late August and in September, so that, as far as possible, all the plantations were sampled when the animals were at the same stage in their life history.

Identification of both nymphs and adults of all the species presented no difficulty with two exceptions. No absolute diagnostic character could be discovered which would separate the nymphs of the two *Amphigerontia* species, *A. bifasciata* and *A. contaminata*. Last instar nymphs were identified by measurement of the flagellar length of female nymphs and of the ratio of head width to interocular distance in male nymphs. The ranges of variation of these characters overlap in the two species but not very extensively. In samples consisting almost entirely of one species, identification could be made with a reasonable degree of certainty. In samples in which both species were frequent, their proportions were estimated by plotting cumulative frequencies against size classes on arithmetic probability paper according to the method described by Harding (1949). All the last instar *Amphigerontia* nymphs collected in the late summer survey were sexed, measured and analysed in this way. The proportions of the two species among the nymphs in earlier instars were assumed to be the same as the proportions of the two species in the adult and last instar nymphal stages at each locality. The *Peripsocus* species will be reported on at a later date, since, although adults are identifiable, their

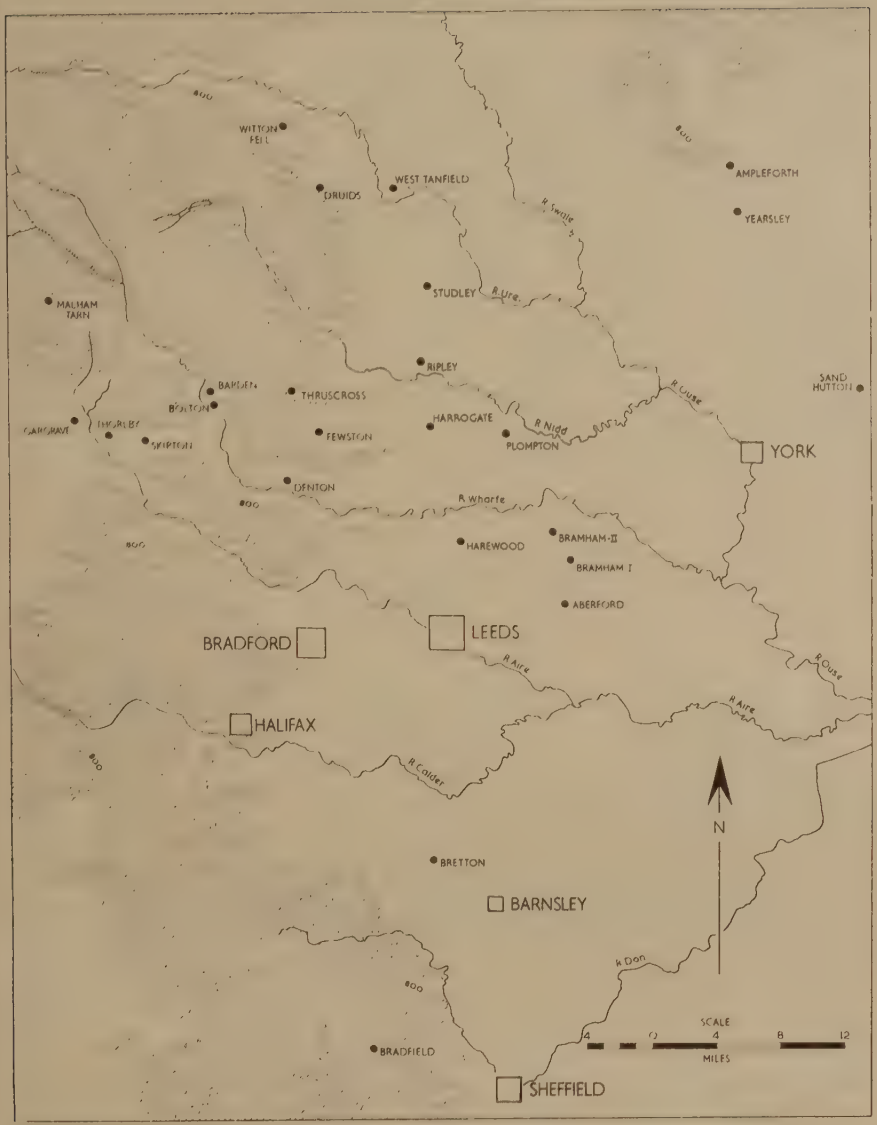

Fig. 3. Map of the Pennine region in Yorkshire to show stations; land above 800 ft stippled.

nymphs cannot be identified to species on present knowledge. Three species are, however, represented in the samples, viz. *P. alboguttatus* (Dalm.), *P. didymus* Roesl. and *P. placopterus* (Steph.), the two latter species being the commonest.

(*b*) *The psocid fauna*

The composition of the psocid fauna in late June and early July is shown in Table 5, where the total captures of adults and late instar nymphs from ten stations at various altitudes from 300-1300 feet above sea level are recorded. 96% of the psocid population is made up of four species. Two of these, *Mesopsocus unipunctatus* and *M. immunis*, are by far the most numerous, and at this period both are represented by nymphs in the third to sixth instars and by recently emerged adults. These individuals have all developed from overwintering eggs. Of the other two species, *Reuterella helvimacula* is represented by adults and late instar nymphs and *Elipsocus hyalinus* by adults only, and all these had evidently emerged from eggs the previous autumn and had overwintered as either adults or nymphs. The remaining species were all in the adult or late instar stage at the time of capture. Very young nymphs of other species and of *Reuterella helvimacula* and *Elipsocus hyalinus* were also appearing at this time but are not recorded in Table 5.

Table 5. *The relative abundance of psocid species on larch in early summer*

The figures show total captures from ten localities, 27 June-4 July 1955. Equal numbers of samples were taken from living and from dead branches.

	Numbers captured from		Total capture on larch	Percentage of total psocid capture
	living twigs	dead twigs		
Mesopsocus unipunctatus	1300	834	2134	53·0
M. immunis	441	858	1299	32·3
Reuterella helvimacula	2	326	328	8·2
Elipsocus hyalinus	23	67	90	2·2
Seven other species*	140	36	176	4·3
Total	1906	2121	4027	100·0

* *Cuneopalpus cyanops* (Rost.), 68 individuals; *Cerobasis guestfalicus* Kolbe, 66; *Loensia fasciata* (F.), 25; *Graphopsocus cruciatus* (L.), 9; *Stenopsocus immaculatus* (Steph.), 5; *Caecilius burmeisteri* Br., 2; and *C. flavidus* (Steph.), 1.

The composition of the psocid fauna in August and early September differs markedly from that in June and early July. Table 6 records the total capture of all individuals, both nymphs and adults, from twenty-four stations at various altitudes between 100 and 1300 ft above sea level. The two *Mesopsocus* species have now all emerged as adults and are rapidly dying out. Of the total psocid population 96% is made up of seven species: *Philotarsus picicornis*, *Reuterella helvimacula*, *Elipsocus westwoodi*, *E. melachlani*, *E. hyalinus*, *Amphigerontia bifasciata* and *A. contaminata*. The majority of the individuals captured were either adults or late instar nymphs. Younger nymphs, however, were taken when

present and are recorded in the table. All individuals of the above-mentioned species present at this time of the year had emerged from eggs in the spring or early summer. They survive as feeding populations until about the end of October, so that apart from the very small numbers of *Reuterella helvimacula* and *Elipsocus hyalinus* surviving the winter as nymphs or adults, there are 5-6 months in the year when little or no food is being taken by psocids. In addition to these nine species, fourteen others are present in very small numbers. Differences between

Table 6. *The relative abundance of psocid species on larch in late summer*

The figures show total captures from twenty-four localities, 8 Aug.-24 Sept. 1954. Equal numbers of samples were taken from living and from dead branches.

	Numbers captured from		Total capture on larch	Percentage of total psocid capture
	living twigs	dead twigs		
Philotarsus picicornis	6356	4274	10 630	26·8
Reuterella helvimacula	406	9394	9800	24·7
Elipsocus westwoodi	5462	824	6286	15·8
Amphigerontia bifasciata	1211	4510	5721	14·4
Elipsocus mclachlani	77	2722	2799	7·0
E. hyalinus	472	1664	2136	5·4
Amphigerontia contaminata	585	158	743	1·9
Mesopsocus unipunctatus	112	55	167	0·4
M. immunis	52	40	92	0·2
Fourteen other species*	991	348	1339	3·4
Total	15 724	23 989	39 713	100·0

* Three *Peripsocus* spp., 792 individuals, *Cerobasis guestfalica* Kolbe, 269, *Stenopsocus immaculatus* (Steph.), 151; *Metylophorus nebulosus* (Steph.), 35; *Psococerastis gibbosus* (Sulz.), 29; *Trichadenotecnum sexpunctatum* (L.), 15; *Lachesilla pedicularia* (L.), 12; *Cuneopalpus cyanops* (Rost.), 8; *Caecilius burmeisteri* Br., 7; *Loensia variegata* (Latr.), 3; *L. fasciata* (F.), 3; *Graphopsocus cruciatus* (L.), 1; and 14 unidentified nymphs.

species in the readiness with which they are dislodged from the twigs by beating introduce an error in these estimates of relative abundance. The removal of individuals from twigs in the laboratory by tapping them sharply has indicated that the two species which spin most silk, and which incidentally are the two most abundant species, *Philotarsus* and *Reuterella*, are those least readily dislodged. Individuals of the other seven common species are easily dislodged by tapping in this manner.

(c) *Nymphal and adult distributions*

In the early summer the psocid population is made up largely of two *Mesopsocus* species, both feeding on *Pleurococcus* and fungal spores. The later summer population is made up largely of five species feeding on *Pleurococcus* and fungal spores, *Philotarsus picicornis*, *Elipsocus westwoodi*, *E. hyalinus*, *Amphigerontia bifasciata* and *A. contaminata*, and two lichenophilous species, *Reuterella helvimacula* and *Elipsocus mclachlani*. The preference experiments reported earlier

in this paper showed that for each of these species the nymphal proportions on the two halves of the composite twig were very similar to the adult proportions. These distributions are determined largely by the individuals' reaction to crowding on the one hand and by their preference for either *Pleurococcus* or lichen on the other. In so far as these factors play a part in determining the distribution of these species in nature, we should expect the nymphs and adults of each species to show the same relative proportions on living and on dead twigs of larch in the field. Table 7 sets out these proportions for both the adults and the nymphs of each

Table 7. *Nymphal and adult distributions on larch*

Proportions on living and on dead twigs are expressed as percentages for adults (upper) and for nymphs (lower figures).

	Percentage			Percentage adults + nymphs	
	on living twigs	on dead twigs	Number of specimens	on living twigs	on dead twigs
Philotarsus picicornis	53	47	1426	60	40
	61	39	9204		
Elipsocus westwoodi	91	9	991	87	13
	86	14	5295		
E. hyalinus	38	62	544	22	78
	17	83	1592		
E. mclachlani	7	93	372	3	97
	2	98	2427		
Reuterella helvimacula	7	93	4785	4	96
	1	99	4274		
Amphigerontia bifasciata	30	70	1014	21	79
	19	81	4707		
A. contaminata	89	11	37	79	21
	78	22	706		
Mesopsocus immunis	52	48	86	34	66
	33	67	1213		
M. unipunctatus	56	44	310	49	51
	45	55	534		

species. The figures for the first seven species are compiled from the total capture from twenty-four localities in the late summer survey in sixty-seven samples from living branches and sixty-seven from dead branches. Those for the two *Mesopsocus* species are compiled from the total capture in the early summer survey from the lowland localities only, where both species were present. The nymphal distribution corresponds reasonably closely to that of the adults for each species. A somewhat larger percentage of the adults is present on the living twigs when compared with the nymphs for all the species except *Philotarsus*. This is probably due not to any difference between the nymphs and the adults in their selection of the habitat, but to the fact that development is more rapid and adults emerge earlier on the living branches which are fully exposed to the sun than on the dead branches under the canopy where cooler conditions prevail. It would appear then that the nymphs of any one species are feeding on the same food and living in the same microhabitat as their respective adults, so that the nymphal and

adult populations of any one species at one place may justifiably be regarded as a single ecological unit with regard to problems of grazing pressure and of the interaction between competing, or potentially competing, species.

The last column of Table 7 summarizes the proportions of the total capture of each species on living and dead twigs, and thus indicates in a general way the differences between these species regarding habitat selection. The two points of interest which arise from this will be mentioned only briefly here since additional data of a more precise nature are presented later. The first relates to the degree of divergence that has taken place in the selection of habitat by the members of each of the three groups of closely related species. In two of these groups this divergence is very marked. Thus *Amphigerontia contaminata* predominates on the living branches whereas *A. bifasciata* is most frequent on the dead ones. Likewise *Elipsocus westwoodi* lives mainly on the living branches whereas *E. mclachlani* is almost completely restricted to the dead branches, with *E. hyalinus* occupying an intermediate position. The degree of overlap of their populations is, however, appreciable. In the third group, the two *Mesopsocus* species show much less divergence than do these others, the spatial overlap of their populations being very extensive. The second point of interest concerns the possibility of relating these relative frequencies on living and dead branches to the food supply. The most striking distributions are those of *Reuterella helvimacula* and *Elipsocus mclachlani*, which are scarcely represented at all in the samples from living twigs. This distribution is understandably related to the distribution of the lichen, which was present on the dead branches in most of the plantations but was rarely present on the terminal portion of living branches, which was the part sampled. The remaining species, all feeders on *Pleurococcus* and fungal spores, nevertheless show varied distributions, suggesting that factors other than the abundance of food play an important part in the selection of the habitat by these several species. Since conditions often varied considerably from locality to locality, these figures representing total capture from many places cannot be related to the distribution of *Pleurococcus* and fungal spores with any precision. Data having a more direct bearing on this problem will be considered in the next section.

(*d*) *Distribution and abundance of the early summer populations*

Changes in population size with altitude are summarized for the early summer psocid fauna in Table 8, where the average numbers of individuals per sample are given for the four common species. The difference between the two *Mesopsocus* species in their response to conditions at the higher altitudes is immediately apparent. Whereas both species are abundant at localities below about 800 feet, only *M. unipunctatus* can maintain populations above this altitude. Nine of the ten stations may be regarded as forming two transects across the eastern slopes of the Pennines, both of them along lines running approximately SE-NW, one in Wensleydale (Tanfield, Druids and Witton Fell) and the other further south in Wharfedale and Airedale (the remaining stations except Bradfield). The pattern of distribution of these two species is the same in both these areas, and in both of

them the edge of the range of *M. immunis* is particularly abrupt. In Wensleydale the sudden drop of the *M. immunis* population to extinction occurs between Tanfield and Druids within a distance of only 4½ miles over which the altitude changes from 300 to 900 ft. In Wharfedale and Airedale, it occurs between Gargrave (500 ft) and Malham Tarn (1250 ft) which are 7 miles apart. These two species are very similar to each other both in size and in body form, the females being apterous and the males fully winged, and their populations are highly

Table 8. *The altitudinal distribution and relative abundance of the early summer psocid populations on larch*

Figures give the average numbers of individuals per sample (10 units) at ten stations; 27 June-5 July 1955.

		Altitude 300-400 ft			Altitude 500-550 ft			Alt. 900 ft	Altitude 1050-1300 ft		
		Harewood	Denton	Tanfield	Bolton	Skipton	Gargrave	Druids	Witton Fell	Bradfield	Malham Tarn
Number of samples	living twigs	5	3	2	2	2	3	3	3	4	3
	dead twigs	5	3	2	2	2	3	3	3	4	3
Mesopsocus immunis	living twigs	1	13	21	104	23	34	0	0	0	0
	dead twigs	0·4	36	54	44	221	37	0	0	0	0
	all twigs	0·8	24	37	74	122	36	0	0	0	0
M. unipunctatus	living twigs	11	15	78	16	11	35	88	81	21	98
	dead twigs	18	21	74	13	30	15	27	82	10	13
	all twigs	15	18	76	15	20	25	58	82	16	55
Reuterella helvimacula	living twigs	0	0	0·5	0·5	0	0	0	0	0	0
	dead twigs	0·4	38	27	78	0	0	0	0	0	0
	all twigs	0·2	19	14	39	0	0	0	0	0	0
Elipsocus hyalinus	living twigs	0·4	2	4	0·5	0	2	0	0	0	0
	dead twigs	2	2	9	2	0·5	7	2	0	0·3	0
	all twigs	1	2	6	1	0·3	5	1	0	0·1	0
All other psocids	living twigs	5	14	2	12	1	1	14	0	0	0
	dead twigs	1	2	2	5	1	2	1	0	0·3	0
	all twigs	3	8	2	9	1	2	7	0	0·1	0

interspersed (Table 7), so that differential predation is unlikely to be the factor responsible for this difference in their distribution. Since both species are equally active and since they occur on many other kinds of tree as well as on larch, the absence of *M. immunis* in the hills cannot be attributed to difficulties of dispersal. Their phenology is also very similar. Both overwinter entirely in the egg stage and the eggs hatch at almost the same time in the spring. The fact that this emergence takes place over a relatively short period in both of them suggests a rigid diapause, so that cooler spring conditions in the hills would not be expected to act differentially at this period in the life history. Nor would the shorter summer season in the hills be likely to be the factor concerned, since most if not all the eggs of both species are laid by the end of August. The most important parasites are Myrmaridae, which have been bred from the eggs of both species.

By this process of elimination it appears that the major factor responsible for the difference in distribution must be looked for in the relative ability of the eggs to withstand the winter climate, about which no information is available at present. The other two species in this early summer census were represented only by individuals which had overwintered either as nymphs or as adults. Both these species are more abundant in the late summer, so that their distribution in the spring can only be discussed with reference to the relative sizes of their late summer populations at the same localities, which are set out in Table 9. In the lowlands, *Elipsocus hyalinus* adults and nymphs are overwintering in appreciable

Table 9. *Average number of individuals per sample (20 units) of* Reuterella helvimacula *and* Elipsocus hyalinus *at 10 stations; 10-31 August 1954*

		Altitude 300–400 ft			Altitude 500-550 ft			Alt. 900 ft	Altitude 1050-1300 ft		
		Harewood	Denton	Tanfield	Bolton	Skipton	Gargrave	Druids	Witton Fell	Bradfield	Malham Tarn
Number of samples	living twigs	4	4	2	4	1	2	3	3	3	2
	dead twigs	4	4	2	4	1	2	3	3	3	2
Reuterella helvimacula	living twigs	0	1	0	2	0	0.5	7	113	0	0
	dead twigs	2	13	127	72	175	11	144	1999	0.3	0
	all twigs	1	7	64	37	88	6	76	1056	0.2	0
Elipsocus hyalinus	living twigs	13	7	7	5	0	9	18	2	7	2
	dead twigs	71	24	11	29	6	18	43	2	21	1
	all twigs	42	15	9	17	3	13	31	2	14	1

numbers (up to nine individuals per sample), but they are very scarce or absent from the samples taken from the three highest localities above 1000 ft. This is partly due to the fact that at two of these highest localities, Malham Tarn and Witton Fell, the population is always small, so that the numbers overwintering will be correspondingly low with the likelihood of missing them entirely in the samples. It is, however, not entirely to be accounted for in this way as the following observations in larch plantations at Malham Tarn (1250 ft) and at Harrogate (500 ft) will show. The life cycle and population dynamics of *E. hyalinus* at Malham Tarn have been worked out in some detail by Broadhead & Thornton (1955). Sampling carried out by them during the winter months produced neither nymphs nor adults, and their absence at this period was confirmed by age-group studies of the summer populations at regular intervals. From their data, it may confidently be asserted that *E. hyalinus* at Malham overwinters entirely in the egg stage; the nymphs emerge between the end of May and the end of June and the successive nymphal instars follow one another during the summer months, the first adults appearing towards the end of August. The course of the life cycle in the lowlands has not been worked out in detail, but samples taken from a larch plantation at Harrogate at various times for other purposes give some information for comparison

with that from Malham. It is not known whether the eggs of this species overwinter in the lowlands, but at the end of May adults and late instar nymphs, which had evidently overwintered in this stage, were present in the field. These nymphs had become adult by the middle of June and all died out towards the middle of July. First instar nymphs were recorded towards the end of June and these became adult from the beginning of August. The most noticeable difference between the course of the life cycle of *E. hyalinus* in the lowlands and that in the hills is the ability of nymphs and adults to overwinter in the lowlands and their inability to do so at the highest locality where plantations are available for study. Similarly in the case of *Reuterella*, apart from an occasional first or second instar nymph unrecorded in Table 8, the species was represented in these samples entirely by adults and a few last (sixth) instar nymphs. Both in Wensleydale and further south in Wharfedale and Airedale, they were present at the localities below about 500 ft and absent from those above this altitude. It should be remarked that, of the three localities at 500-550 ft, Skipton and Gargrave, at both of which *Reuterella* is recorded as absent at this time of the year, are situated further within the Pennines than is Bolton, where it is present, and their climate no doubt approximates more closely to that at higher altitudes. Since young nymphs have been taken as late as October, these adults and last instar nymphs captured at the lower localities at the end of June had probably lived through the winter as nymphs. At four of the six localities in the hills, at which this species is recorded as absent in the early summer, it is abundant later in the season (Table 9), so that here it overwinters entirely in the egg stage. The captures from all ten localities on both occasions, recorded in Tables 8 and 9 respectively, were made from the same plantations and often from the same group of trees. This distributional pattern therefore indicates that nymphs are able to survive throughout the winter in the lowland areas but cannot do so in the hills, where the species overwinters in the egg stage only, and it suggests that winter climate is the factor involved. The population consequences of this difference in the course of the life cycle in the lowlands and in the hills in both *Elipsocus hyalinus* and *Reuterella helvimacula* can only be assessed when more information is available on their population dynamics in both these areas, but whereas *Elipsocus hyalinus* is slightly less numerous at localities above 1000 ft than it is in the lowlands, *Reuterella* is very much more abundant in the hills than at lower altitudes (Table 10). In the former species, climatic conditions are probably responsible for this difference in population levels, but in the case of *Reuterella*, food supply is probably the most important factor.

(*c*) *Distribution and abundance of the late summer populations*

Changes in population size with respect to altitude are summarized for the late summer psocid fauna in Table 10, in which the average capture per sample is recorded for each species at the twenty-four localities, here grouped into five categories of altitude. The two lichenophilous species, *Elipsocus mclachlani* and *Reuterella helvimacula*, and the three most abundant species which feed on *Pleurococcus* and fungal spores, *Philotarsus picicornis*, *Elipsocus westwoodi* and

Amphigerontia bifasciata, each show a pronounced increase in density with increasing altitude. These five species together make up 89% of the total psocid population at this time of the year. The population level of *Elipsocus hyalinus* remains relatively constant throughout except for a slight and probably significant decrease at altitudes above 1000 ft. *Amphigerontia contaminata*, which is by no means as common as these other species, shows no regular population change with change in altitude, and its relatively high density at 100-250 ft and at 1000-1300 ft is due largely to its great abundance at two localities only, Aberford (200 ft) and Malham Tarn (1250 ft). It is noted here along with the abundant species primarily to indicate the difference between the two closely related *Amphigerontia* species in this respect.

Table 10. *The altitudinal distribution and relative abundance of the late summer psocid populations on larch; 8 Aug.-24 Sept. 1954*

Figures give the average numbers of individuals per sample (20 units) at twenty-four stations grouped into five categories of altitude.

Altitude range (ft)	Number of samples	*Elipsocus westwoodi*	*E. hyalinus*	*E. mclachlani*	*Reuterella helvimaculc*	*Philotarsus picicornis*	*Amphigerontia bifasciata*	*A. contaminata*	All other species	Total psocids
100-250	36	21	20	0	8	13	5	10	4	82
300-450	44	10	18	0·02	24	57	16	0·4	13	138
500-550	20	14	11	1	25	89	57	0·7	21	218
600-900	18	54	17	28	89	103	64	0·7	19	374
1000-1300	16	240	6	142	396	253	159	20	8	1225

Differences in altitude are associated with differences in climate, which can be illustrated, though only in a general way, by rainfall data. Annual rainfall figures for the precise localities at which sampling was carried out are not available, but they have been estimated (Table 12) from the isohyet map of mean annual rainfall for the period 1881-1915 (Meteorological Office 1949). These are of course not realistic figures for comparison with psocid population densities. At most they provide a rough index of climatic factors more directly involved such as the humidity of the microhabitat of nymphs and adults during the late spring and the summer; the temperature, in winter as well as in summer, may also be important. They do, however, illustrate the increasing amount of rainfall with increasing altitude, varying from about 25 in. at the lowest localities to about 60 in. at the highest, Malham Tarn. The variation in amount of rainfall from year to year is considerable. Thus at Malham Tarn annual rainfall in the years 1949-54 varied from 53 in. in 1952 to 77 in. in 1954, the year when this late summer survey was carried out. The fact that the change in population level with changing altitude is of a similar nature in each of the five commonest psocid species suggests that climate is the major ultimate factor setting an upper limit to population size, since it is extremely unlikely that predator and parasite action would be so graded as to produce this effect in all these species. Climate may produce this gradation in

population size in several ways. In the first place, it may exert a direct effect. Broadhead & Thornton (1955) showed that the three *Elipsocus* species are adversely affected by humidities below about 70% R.H. for long periods but on a sunny day in July at Malham Tarn the relative humidity at the twig surface fell below this figure for only 3-3½ h. Humidities are presumably lower in the lowland areas of lower rainfall, but whether these are low enough over a sufficiently long period to affect mortality- and oviposition-rates is not known. The effect of periodic exceptionally dry summers on the population levels reached in succeeding years may be even more important, however, in species which have only one generation per year, especially if their reproductive potential is not very great. In the second place industrial pollution of the air may affect psocid populations either because they ingest the deposit on the twigs or indirectly through its effect on the food supply. This is no doubt an important factor in cities where pollution levels are high, but such pollution falls off very rapidly even within a city boundary over a distance of a few miles from the main source of pollution (Saxton 1952) Although no figures are available for the rural districts, the amount of pollution is certainly very small throughout the whole area to the north and north-west of Leeds, within which most of the localities sampled are situated. Since, moreover, the localities in each of the five altitude groupings of Table 10 are fairly widely scattered over this area, it is considered highly unlikely that a pollution gradient, even if present, is contributing to this observed gradient in psocid population levels. Thirdly, climate may be exerting its main effect on these psocid populations indirectly through the food supply. There is little doubt that the damper conditions in the hills, especially in summer when these animals are actively feeding, promote a more rapid growth and regeneration of the food. The increasing abundance of lichen on dead larch branches with increasing altitude was particularly noticeable when this survey was being carried out. At localities above about 700 ft, lichen usually formed a complete cover over the upper surface of the dead branches near the edges of the plantations, and in less dense stands within the plantation itself. At the lowest localities the dead branches carried only small amounts of lichen, evidently owing to the drier conditions which prevailed here, since in these plantations it was often more abundant in sheltered spots where air flow was reduced and the atmosphere consequently damper. Very probably then, the gradient in population density with altitude in the two lichenophilous species is determined by this corresponding gradient in abundance of lichen, the amount of food present determining the upper limit of population size. That these two species cannot maintain populations in nature in the absence of lichen is indicated by the virtually complete restriction of their populations on larch to the lichen-covered dead branches (Table 7). At the lower altitudes, where lichen occurs more sporadically on the dead branches, the proportion of the total food supply present which can be utilized by these species will depend largely on their ability to seek out the isolated patches of food. Neither species would appear to be active searchers, however. Both of them are fairly sedentary and gregarious. The nymphs of *Elipsocus mclachlani* tend to aggregate in small clusters when they are not

feeding and both adults and nymphs of *Reuterella helvimacula* construct silken tents within which they spend most of their time. This lack of mobility no doubt contributes in a significant way to the reduction of their populations in the lowland areas where lichen is less abundant. *R. helvimacula* penetrates much further into these lowland areas than does *Elipsocus mclachlani* which is completely absent at localities below about 500 ft with a rainfall of less than about 35 in. (Table 12). This difference between the two species in distribution pattern is probably due to the difference in food habits already described. *Reuterella* grazes the whole surface of the lichen whereas *Elipsocus mclachlani* feeds only on the fructifying cups. A greater scarcity, involving a more discontinuous distribution of the lichen on dead larch branches will therefore have a more adverse effect on *E. mclachlani* than on *Reuterella*, since small patches of lichen providing sufficient food for the latter will provide much less food in the form of apothecia for *Elipsocus mclachlani*. This may account for the absence of this species in the lowlands, where *Reuterella* is nevertheless able to maintain itself, although the direct effect of climate, in particular the effect of lower humidities in the lowlands, may be a contributory factor. *Reuterella* in its silken tents will be much more protected than *Elipsocus mclachlani* from such a possible cause of mortality. It is not possible to say definitely whether *Pleurococcus* and bark fungi were more abundant in the hills than in the lowlands on the living branches when this survey was being done. The fungal spores are only noticeable when present in a fairly thick layer on twigs infested with *Adelges*, and a thin layer of *Pleurococcus* may easily be overlooked. The impression was gained that *Pleurococcus* was not noticeably more abundant in the hills at this time of the year, but it should be remembered that grazing pressure at the three highest localities was about fifteen times greater than that at localities between 100 and 250 ft, and that the numbers of psocids which can be maintained will depend not so much on the absolute amount of *Pleurococcus* present at any one moment, as upon its growth and reproductive rate. Moreover, the survey was carried out during an unusually wet summer when the differential effect of altitude would be much smaller than in seasons of low or average rainfall. It is suggested then that this gradient in population size in so many of the common psocid species is causally related to the gradient in climatic conditions, and that climate is acting upon these populations through their food supply, although its direct effect on mortality- and oviposition-rates may also be a contributing factor.

(f) The distribution pattern of living and dead larch branches

Since the difference in climate between the hills and the lowlands is responsible for a considerable difference in the size of psocid populations, it is of interest to know whether there are corresponding differences in the distribution of each species on living and dead larch branches in these two areas. Table 11 sets out for each species the proportion of the total capture (in equal numbers of samples from living and dead twigs) found on the living twigs in the lowland localities, and the proportion at higher altitudes. Apart from *Elipsocus mclachlani*, of which the small capture at localities below 550 ft gives an unreliable estimate for comparison, and

Mesopsocus immunis which is entirely absent in the hills, all the species show a broadly similar distribution in both lowland and highland areas. In each case, however, the proportion of the total population occurring on living twigs is smaller in the lowlands. This is probably to be ascribed not to any interactions between species, but to differences in the distribution of the food. Lichen is more abundant in the hills, where it occurs not only on the dead branches of larch but also on the thicker basal portion on the living branches. Although the terminal portions of these living branches were beaten to obtain the samples, some individuals from

Table 11. *Captures of the eight commonest psocid species from larch twigs in the lowlands and the hills*

Figures show the percentage of the total captures (in equal numbers of samples from living and dead twigs) found on the living twigs. (The total numbers of insects are shown in parentheses).

	Aug.-Sept. 1954		June-July 1955	
	16 stations below 550 ft	8 stations above 600 ft	6 stations below 500 ft	4 stations above 900 ft
Number of samples	100	34	34	26
Elipsocus westwoodi	83 (1471)	88 (4815)	–	–
E. hyalinus	21 (1722)	29 (414)	–	–
E. mclachlani	15 (27)	3 (2772)	–	–
Reuterella helvimacula	1·5 (1113)	4·6 (7946)	–	–
Philotarsus picicornis	53 (4731)	66 (5899)	–	–
Amphigerontia bifasciata	10 (2034)	27 (3687)	–	–
Mesopsocus immunis	–	–	34 (1299)	0
M. unipunctatus	–	–	49 (844)	69 (1290)

the thicker lichen-covered portion were inevitably taken, and this would result in the larger proportion of *Reuterella* on living twigs at localities above 550 ft. *Pleurococcus* is relatively scarce on dead branches in the hills but more frequent on dead branches at lower altitudes, and this may account for the fact that a greater proportion of the populations of the *Pleurococcus* and fungal spore feeders is to be found on the dead twigs in the lowland region.

(g) *The coexistence of species exploiting a common food resource*

Table 12 summarizes, by means of an arbitrarily defined scale, the relative abundance of the lichenophilous species and of the species feeding on *Pleurococcus* and fungal spores at each of the twenty-four localities during the late summer survey of 1954. It is probable that the data for all these species, except *Reuterella helvimacula* and possibly *Amphigerontia contaminata*, refer to populations which have achieved some measure of balance and which are not merely in a transient stage of colonization. This is certainly true for *Elipsocus westwoodi*, *E. hyalinus* and *Philotarsus picicornis*, which are recorded from all stations. The recorded absence of *Elipsocus westwoodi* from Yearsley, where it no doubt occurs, can be ascribed to sampling error. The stations at which *Amphigerontia bifasciata* is recorded as absent are all in the lowlands where this species is generally much scarcer than at higher altitudes, so that these recorded absences are unlikely to be due to the

Table 12. *Relative abundance of the seven commonest psocid species on larch at twenty-four localities, 8 August–24 September 1954*

Symbols show the average number of individuals per sample of 20 units (from living or dead twigs): –, absent; l, <10; m, 10-100; h, >100.

			Lichen feeders		Species feeding on *Pleurococcus* and fungal spores						
	Altitude (ft)	Approx. annual rainfall (in.)	*Elipsocus mclachlani*	*Reuterella helvimacula*	*Elipsocus westwoodi*	*E. hyalinus*	*Philotarsus picicornis*	*Amphigerontia bifasciata*	*A. contaminata*	Number of species at 'high' density	Number of species at 'moderate' or 'high' densities
Sand Hutton	100	25	–	l	m	m	m	–	–	0	3
Plompton	200	27	–	–	m	m	l	l	l	0	2
Aberford	200	26	–	–	m	l	l	l	m	0	2
Bramham I	250	26	–	h	m	m	m	m	–	0	4
Bramham II	200	26	–	l	l	m	l	–	–	0	1
Bretton	300-450	30	–	–	l	l	l	–	l	0	0
Harewood	350-400	29	–	l	m	m	l	l	–	0	2
Ripley	300-350	29	–	h	m	m	l	–	–	0	2
Denton	350	34	–	m	m	m	h	l	–	1	3
Studley	250-300	30	l	l	m	m	h	h	–	2	4
Tanfield	300	29	–	h	l	m	h	m	–	1	3
Bolton	500	40	l	m	m	m	m	l	–	0	3
Skipton	550	37	–	h	l	l	h	h	l	2	2
Thorlby	500	36	–	–	h	m	h	h	l	3	4
Gargrave	500	35	l	m	l	m	m	l	–	0	2
Yearsley	500	29	–	–	–	m	m	m	–	0	3
Fewston	600	38	l	h	m	m	m	m	–	0	4
Thruscross	700-750	40	m	h	h	m	h	h	l	3	4
Barden	750-800	42	m	–	m	l	l	l	–	0	1
Ampleforth	750	30	m	–	m	l	m	m	l	0	3
Druids	900	36	m	h	h	m	h	h	–	3	4
Witton Fell	1050	37	l	h	h	l	h	h	m	3	4
Bradfield	1100	45	m	l	h	m	m	l	l	1	3
Malham Tarn	1250-1300	60	h	–	h	l	h	h	m	3	4
Number of localities at which species was present			11	16	23	24	24	20	10		

species having failed to reach these plantations. No reliable conclusions can be drawn from the data for the much rarer *A. contaminata*. There has then evidently been sufficient time available for the colonization of these larches, 30-50 years of age, by these species feeding on *Pleurococcus* and fungal spores, all of which occur on other tree species never very far distant from the larch plantations. *Pleurococcus* and bark fungi are present on larch trees at a very early age, but lichen does not appear in quantity until the lower branches die off when the tree is at least 12-15 years old. The time available for colonization by the lichenophilous species is therefore much less. Nevertheless the pattern of abundance of *Elipsocus mclachlani* suggests that its scarcity or absence in the lowlands cannot be accounted for by difficulties of dispersal of individuals to these lowland plantations. *Reuterella helvimacula*, however, provides a marked contrast. Although the general trend of increasing density with increasing altitude is apparent, this species is nevertheless sporadic in its occurrence, and the pattern of its recorded absence bears no relation to altitude. Its sedentary habits have already been noted. Moreover, the adult females are wingless, and its distribution within any one plantation, unlike that of the other species, is often very patchy indeed. Its recorded absence at many of the stations is therefore to be ascribed to this slow rate of dispersal rather than to its inability to maintain populations there. It may be noted here that *Reuterella* is entirely absent from the woodlands around Malham Tarn, which have been intensively studied and where conditions are certainly very favourable to it. With these considerations in mind, the feeders on *Pleurococcus* and fungal spores are of more immediate interest than the lichenophilous species regarding problems arising from the coexistence of species exploiting a common resource, as, for instance, that of interspecies competition.

Up to four of the species that feed on *Pleurococcus* and fungal spores occurred at moderate or high densities on the same trees and at the same time in the latter half of the summer in almost all these plantations (Table 12). At five localities three of these four species, *Elipsocus westwoodi*, *Philotarsus picicornis* and *Amphigerontia bifasciata*, were living together at high population densities. The fourteen other species, which together make up 3·4% of the total population (Table 6) were also feeding at this same period. Four of them, *Peripsocus phaeopterus* and *P. didymus*, *Cerobasis guestfalicus* and *Stenopsocus immaculatus*, were present at moderate densities in some of these plantations, and an examination of gut contents indicates that these also feed on *Pleurococcus* and fungal spores. In addition to these, populations of *Mesopsocus unipunctatus* at the localities above about 800 ft and populations of both *M. unipunctatus* and *M. immunis* at the lower localities had been grazing this food earlier in the season. This widespread coexistence of several species exploiting this common food resource suggests that it is a situation of some permanence and stability.

ABSOLUTE POPULATION DENSITIES AND GRAZING PRESSURE

So far, only population density indices obtained by means of the beating technique of sampling have been considered. These can give little or no indication

of grazing pressure, and they illustrate the spatial overlap between the various species populations only in a general way. Measurement of absolute population densities, such as the number of individuals per unit length of larch twig, will give some preliminary indication of how intense the grazing pressure is likely to be at any one time; it will also give a more precise indication of the degree of interspersion of these populations. Moreover, by comparison of such data from a highland locality with that from a lowland locality where both lichen and *Pleurococcus* are distributed on a larch tree in a different way, the extent to which the distribution of the food determines the distribution of the animals may be assessed.

(*a*) *Late summer populations*

The population densities of those species which make up the late summer psocid fauna will be considered first, by reference to two localities at a high altitude and to one lowland locality.

Two highland plantations were studied in order to obtain density figures for all the common species. These were the small isolated plantation of immature larches on the top of Witton Fell at 1050 ft and a pure larch stand in the Ha Mire plantation bordering Malham Tarn at 1250 ft. Living and dead larch twigs, all about 5 mm in diameter, were sleeved in a 25 cm test tube, the twig cut off and the tube corked. The psocids on them were removed and counted in the laboratory. The twigs were chosen for greatest homogeneity of bark flora and to present the maximum contrast between living and dead twigs. Only those living twigs were chosen which had at least 90% of their upper surface covered with *Pleurococcus* and fungal spores and carried only very small amounts of lichen. The latter occupied on average only 3% of the upper surface of the twigs from Malham and less than 1% of the upper surface of those from Witton, and comprised young non-fructifying thallus. In all cases, the bark flora consisted of a mixture of *Pleurococcus* and fungal spores, but at Witton, where the trees were heavily infested with *Adelges*, the fungal spores predominated in this relatively thick blackish green layer covering the bark, whereas at Malham *Pleurococcus* was far more abundant than the fungal spores and the mixture was present on the twigs in a much thinner and greener layer. The dead twigs, taken as samples, were all completely covered on their upper surface with fructifying lichen (*Lecanora conizaeoides*) with little or no trace of *Pleurococcus* visible. This lichen formed only a thin layer less than 1 mm thick on the twigs at Witton, evidently the result of the long continued heavy grazing of the dense *Reuterella* population there, but at Malham, where *Reuterella* is absent, the more selective grazing of *Elipsocus mclachlani*, which leaves the thallus untouched, has allowed the formation of a layer of this lichen 2-3 mm thick on the dead larch branches.

The total number of psocids on thirty 25 cm lengths of each kind of twig at Witton and twenty-six of each kind at Malham are recorded in Table 13. The Witton populations were the densest recorded, averaging 7·7 individuals per 10 cm length of living twig and 5·9 per 10 cm of dead twig. Almost all these individuals were in the last nymphal or the adult stages and therefore quite large. Grazing here

was obviously intense. The species were distributed as would be expected from the laboratory preference experiments, the great majority of the feeders on *Pleurococcus* and fungal spores occurring on the living twigs, although a relatively large proportion of the *Amphigerontia bifasciata* was present on the dead ones. Most of the *Reuterella* population was on the dead twigs, all in small clusters under silken tents in the axils of the short side shoots. Of the 622 side shoots present on these 750 cm of dead twig, 172 were occupied by this species, and in these axils the lichen was grazed down either to the white medulla or in a few cases to

Table 13. *Interspersion of psocid populations on larch trees at two highland localities*

Figures show the total numbers of individuals on thirty 25 cm lengths of twig of each kind at Witton Fell on 28 Aug. 1954, and on twenty-six 25 cm lengths of each kind at Malham Tarn on 30 July 1954.

	Witton Fell		Malham Tarn	
	Living twigs	Dead twigs	Living twigs	Dead twigs
Philotarsus picicornis	364	32	139	1
Amphigerontia bifasciata	32	20	71*	17*
Elipsocus westwoodi	117	14	51	11
E. mclachlani	–	–	1	160
E. hyalinus	–	–	0	1
Reuterella helvimacula	62	372	–	–
Peripsocus sp.	2	1	–	–
Mesopsocus unipunctatus	–	–	5	0
Total psocids	577	439	267	190

* Including *A. contaminata*

the bark itself. Elsewhere on these twigs little grazing was noticeable. At this time of the year, then, there would appear to be no shortage of resting place or food for this species at Witton, but it should be remembered that unlike the other species *Reuterella* has a second generation later in the summer, so that grazing pressure and its cumulative effect over the whole season are likely to be maximal at the end of September. It may be noted here that individuals from these twigs were used for the gut content analysis recorded in Table 4. The *Reuterella* found on the living twigs had been feeding entirely upon *Pleurococcus* and fungal spores, so that in all these samples from Witton, 577 individuals were feeding upon these foods on the living twigs and 67 were taking these foods together with a small proportion of lichen from the dead twigs. There were 372 individuals eating lichen alone on the dead twigs and none on the living twigs, these 372 individuals, all *Reuterella*, being smaller than those of the other species. On these twigs, therefore, there are almost twice as many individuals feeding on the layer of *Pleurococcus* and fungal spores as there are feeding on a layer of lichen of the same area and of about the same thickness. It is probable that under favourable conditions the growth-rate of *Pleurococcus* is much greater than that of lichen.

The psocid populations at Malham on 30 July 1954 were less dense than those at

Witton on 28 August 1954 and they would no doubt have been smaller still a month later, since all the species concerned have only one generation a year. The total psocid population at Malham averaged 4 individuals per 10 cm length of living twig and 2·9 per 10 cm of dead twig. Apart from the five *Mesopsocus unipunctatus* adults, these individuals were all in the second to fifth instars, so that it was not possible to identify the *Amphigerontia* nymphs to species. Both *A. bifasciata* and *A. contaminata* were present in this plantation a month later in the proportion of about 3 : 1. Allowing for the difference in density, the distribution of these species at Malham corresponds reasonably closely to the distributions obtained in the preference experiments, in which the twigs used, although dead, were very similar in their covering of *Pleurococcus* and lichen to those sampled at Malham. It would appear, then, that at these high localities the distribution of the food on a larch tree determines to a large extent the distributional pattern of the various psocid species.

The locality chosen for study as representative of conditions in the lowlands was a larch plantation at Harrogate at an altitude of 500 ft at the edge of the Vale of York. The distribution of the food on the trees here differed considerably from that at Witton Fell and Malham. Lichen was present in much smaller amounts, only one of the lichenophilous species, *Reuterella helvimacula*, being present and this was not abundant. Interest centres, therefore, on the feeders on *Pleurococcus* and fungal spores in this plantation, where *Pleurococcus* for the most part mixed with fungal spores is as abundant on the dead branches as it is on the living ones. Larch twigs in 25 cm lengths were taken in the manner already described. Four kinds of twigs were sampled: living and dead twigs with the bark surface clean apart from small patches of *Pleurococcus* on some or all of the short lateral shoots, and living and dead twigs with at least 80% of the upper surface covered with *Pleurococcus*. These were all taken from branches 2-6 ft above ground level. The living clean twigs were taken from the edge of the plantation, and the other three kinds from a more shaded situation either immediately below the living clean twigs or just within the canopy. The clean bark surface of the upper sides of almost all the dead clean twigs was the direct result of psocid grazing, and the abundance of this type of twig clearly indicates in a general way the intensity of such grazing in this plantation. On each of the 9 days on which sampling was carried out during the period 9 July-7 August 1954, equal numbers (between 14 and 24) of each kind of twig were taken from the same group of trees, and different groups of trees were sampled on different days. A total of 656 twigs, each of length 25 cm, was taken, comprising 4100 cm of each of the four kinds of twigs, and the numbers of individuals of each psocid species and of the possible predators present on each kind of twig are given in Table 14. *Graphopsocus cruciatus* and the two *Mesopsocus* species were represented entirely by adults. These two *Mesopsocus* species, common in the early samples, became progressively less numerous during this survey period and were absent from the samples taken on 7 August. The other species, *Elipsocus hyalinus*, *E. westwoodi*, *Philotarsus picicornis* and the only *Amphigerontia* species present in this plantation, *A. bifasciata*, were all represented by individuals in

instars from the first to the sixth at this time, the majority being second to fifth instar nymphs.

The density of psocids on these larch trees at Harrogate was much less than that at Witton Fell, the average number of individuals per 10 cm length of living *Pleurococcus*-covered twig being 1·2 at Harrogate compared with 7·7 at Witton a month later (Table 13). The correspondence already noted between the distribution of the psocids and that of their food at Witton is by no means so clearly marked

Table 14. *Interspersion of psocid populations on larch trees at Harrogate, 9 July–7 August 1954*

Total numbers of individuals on 164 25 cm lengths of twig (4100 cm) of each kind

	Living twigs		Dead twigs		
	'clean'	'with *Pleuro-coccus*'	'with *Pleuro-coccus*'	'clean'	Total number
Mesopsocus spp.	42	61	35	60	198
Elipsocus hyalinus	2	32	46	113	193
E. westwoodi	62	155	54	21	292
Philotarsus picicornis	40	225	144	137	546
Amphigerontia bifasciata	0	29	161	104	294
Graphopsocus cruciatus	4	0	2	0	6
Total psocids	150	502	442	435	1529
Possible predators:					
Mite, *Anystis baccarum* (L.)	24	46	15	11	96
Spiders	15	7	0	1	23
Syrphid larvae	6	4	4	0	14
Lacewing larvae	8	5	0	0	13
Harvestmen	4	0	1	0	5
Ladybirds	3	1	0	0	4
Empids	1	0	0	0	1
Total predators	61	63	20	12	156

at Harrogate. Fig. 4 shows the proportion of the total capture present on each kind of twig for each of these four species, and the corresponding distributions of the food and of the four species together. Only a small proportion of this total psocid population occurs on the living clean twigs which are those most exposed to sun and wind. The rest of the population is divided up almost equally between the other three kinds of twigs, on each of which the density of individuals is the same. Of all the food on these twig samples 98% was present on half of them, those twigs covered with *Pleurococcus*. The most striking discrepancy, therefore, between the pattern of distribution of food and of total psocids on these twigs lies in the relatively large numbers of individuals on the dead clean twigs, and almost all these individuals belong to three of the four species. The populations of *Elipsocus westwoodi* and *Philotarsus picicornis* are particularly highly interspersed, 40–50% of the populations of each being on the living *Pleurococcus*-covered twigs. The least overlap is between the two closely related species of *Elipsocus*, *E. westwoodi* being

more frequent on the living than on the dead twigs, and *E. hyalinus* being more numerous on the dead ones. At Witton Fell and at Malham, where the living twigs carry *Pleurococcus* and the dead twigs are almost completely lichen covered, the presence of *Elipsocus westwoodi* on the living twigs suggested that its distribution on a larch tree was determined chiefly by the distribution of the food. Its distribution at Harrogate, as well as a comparison of the distributions of all four species here suggests that factors other than food are also likely to be involved in habitat selection.

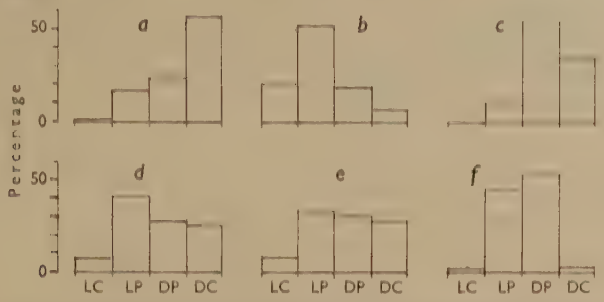

Fig. 4. Proportional distributions of the four commonest late summer psocid species and of their food over four types of larch twig; Harrogate, 9 July - 7 Aug. 1954. *a*, *Elipsocus hyalinus*; *b*, *E. westwoodi*, *c*, *Amphigerontia bifasciata*; *d*, *Philotarsus picicornis*; *e*, the four species; *f*, food. L, living, D, dead twig; P, >80%, C, <4% of upper surface of twig covered with *Pleurococcus*-fungal spore mixture.

(*b*) *Laboratory experiments on* Elipsocus westwoodi *and* E. hyalinus

The purpose of these experiments was to find out whether these species that feed on *Pleurococcus* and fungal spores would react in different ways when they were each presented in the laboratory with simplified but identical environments involving a choice. The two species with the most contrasting distributions on the larch trees at Harrogate were chosen for study, *Elipsocus westwoodi* and *E. hyalinus*. The experimental results may then be compared, in a general way, with the field distributions.

Composite twigs were made up by joining end to end a 10 cm length of living larch twig from which the needles had been removed and a 10 cm length of dead larch twig. The three types of composite twig used were: a living clean twig joined to a dead twig covered with *Pleurococcus* (LC-DP), a living twig joined to a dead twig, both of which were covered with *Pleurococcus* (LP-DP), and a living twig covered with *Pleurococcus* joined to a dead clean twig (LP-DC). The clean twigs carried only very small patches of *Pleurococcus* on the short side shoots, the bark of the twig itself being clean. The other twigs carried a complete cover of *Pleurococcus* on the upper surface. They approximated, therefore, quite closely to the four kinds of twig sampled at Harrogate and were obtained from this same plantation. All the twigs were of the same diameter, about 5 mm. A group of twelve to fourteen fifth to sixth instar nymphs of *Elipsocus westwoodi* was placed on each of twenty-four composite twigs, eight of each of the three types, and a

parallel series was run using *E. hyalinus* nymphs. The twigs were accommodated, as in earlier preference experiments, in pairs in circular glass tanks, one of the composite twigs of each pair being reversed in relation to the other. They were all placed at right angles to the diffused light from a screened window. Humidity was maintained at almost 100% R.H., and room temperature varied between 17° and 21° C. After two days, the number of nymphs on each half and the number of faeces under each half of the composite twig were recorded.

The whole series of experiments was repeated, using adult females instead of nymphs, fourteen females being placed initially on each composite twig and only four replicates being set up instead of eight, for each type of composite twig for each species. These experiments were run for a 3 day period, at the end of which egg counts were recorded, as well as the distributions of adults and faeces.

Table 15. *Preference experiments with* Elipsocus *using three types of composite twig*

Nymphs		Percentage on living half of composite twig	
Species	type of twig	nymphs	faeces
E. hyalinus	LC-DP	43·8	53·1
	LP-DP	56·7	63·4
	LP-DC	85·9	83·4
E.westwoodi	LC-DP	62·7	60·8
	LP-DP	74·5	72·5
	LP-DC	83·7	83·4

Adults				
		adults	faeces	eggs
E. hyalinus	LC-DP	2·9	24·3	9·1
	LP-DP	52·9	54·4	37·2
	LP-DC	66·7	66·6	62·0
E. westwoodi	LC-DP	23·8	21·7	4·5
	LP-DP	53·7	64·6	57·8
	LP-DC	87·3	88·8	79·2

Individuals dropping or flying from the twigs during the experiment were discarded, so that, on average, eleven nymphs per composite twig and ten adults per twig remained at the end of the experiment.

The proportions of individuals, faeces and eggs present on the living half of the composite twig, expressed as percentages, are set out in Table 15 for the nymphs and for the adults of each species on each type of composite twig. As would be expected, the distributions of the faeces are very similar to those of the individuals themselves, this correspondence being reasonably close throughout except for the anomalous and unreliable figure of 2·9 for adult *E. hyalinus* on the first type of twig, only one of the thirty-four adults being on the living half at the end of the experiments. The consistently lower proportion of eggs on the living half, compared with the proportions of individuals and faeces is perhaps due to

the high density of adult females on these twigs. The figures for *E. westwoodi* are in most cases greater than the corresponding figures for *E. hyalinus*. They show that, while the distribution of the food is an important factor in determining the distribution of these species, the nature of the twig itself, that is whether it is living or dead, is also of significance in the animals' selection of the habitat. The response to this latter factor is indicated by the distributions on the second type of composite twig (LP-DP), on both halves of which the food is the same, and may be estimated quantitatively by the deviations of the percentages from the value of 50% expected on the assumption of random distribution. *E. hyalinus* shows for the most part only a slight preference for the living twig, with deviations of 13·4 and 4·4 for the faecal counts for nymphs and adults respectively, and it lays more eggs on the dead twigs than on the living. *E. westwoodi* on the other hand shows a consistent and decided preference for the living twig, the corresponding deviations being 22·5 and 14·6. The response to the distribution of the food may be estimated in each case by the differences between the percentage value for the LP-DP composite twig and each of the values for the other two twig types. In the case of the faeces of nymphal *E. westwoodi* these differences are 11·7 and 10·9, mean 11·3. These two deviations will be the same if the animals react in the

Table 16. *Indices based on faecal counts of the relative importance of the nature of the twig (living or dead) and the distribution of food in determining the distribution of* Elipsocus hyalinus *and* E. westwoodi *in the laboratory preference experiments*

	Nymphs		Adults	
	Twig	Food	Twig	Food
E. hyalinus	13·4	15·2	4·4	21·2
E. westwoodi	22·5	11·3	14·6	33·6

same way to the living or dead condition of the twig regardless of whether or not it is covered with *Pleurococcus*. This is so for the distributions of individuals and faeces for the nymphs of *Elipsocus westwoodi*, for the adult females of *E. westwoodi* and for the eggs of *E. hyalinus*, but not in the remaining six comparisons. The mean values, however, do give an approximate indication of the response of the animals to the distribution of the food in these experiments. They are compared in Table 16, with the estimates of the response to the nature of the twig itself. In these experiments the living or dead condition of the twig exerted an appreciable effect on the distribution of the psocids, this effect being greater for the nymphs than for the adults in both species, and greater for *E. westwoodi* than for *E. hyalinus*.

The differences in response to the experimental twigs are such that a greater proportion of *E. westwoodi* than of *E. hyalinus* (both nymphs and adults) is present on the living twigs. This is also the case for the nymphal distributions in the field (Fig. 4). A part, therefore, at least, of the difference between the patterns of distribution of these two species in the field is the result of differences between them in their inherent response to the environment, uninfluenced by the presence

of other kinds of animals. More direct comparison between laboratory and field data can only be very tentative, since the density of individuals on the experimental twigs (10-13 per 20 cm length of twig) is very much greater than that in the plantation, where the total psocid density averages only 3 per 30 cm length of twig, and also since the animals in the field have, theoretically at least although not entirely in practice, a free choice between the four kinds of twigs sampled, whereas in the experiments these twigs were presented to them only in pairs and allowed only a limited movement as well. However, the field data recorded in Table 14 may be converted into percentage proportions to allow comparison with the laboratory results in Table 15. These are for *E. westwoodi*: LC-DP 53·4%, LP-DP 74·2% and LP-DC 88·1%, and for *E. hyalinus* 4·2, 41·0 and 22·1% respectively. These figures for *E. westwoodi* show good agreement with the laboratory results, but those for *E. hyalinus* are widely different, the proportions on the dead twigs in the field, especially the dead clean ones, being greater than would be expected from the laboratory results. This suggests that in the field *E. hyalinus* responds to factors other than the condition of the twig itself and the amount of food present on it. It is unlikely that the direct influence of the presence of individuals of other species on these twigs at Harrogate produced any spatial displacement of the *E. hyalinus* populations, since densities were relatively low.

(*c*) *Early summer populations*

The absolute population densities of the two species of *Mesopsocus*, which make up the greatest part of the early summer psocid fauna, have been measured at a lowland locality only, since only one of these species is present at the higher altitudes. Sampling was carried out in the same plantation at Harrogate as on the previous occasion in July-August 1954 when the densities of the late summer species were recorded. The same sampling technique was employed. *Pleurococcus* predominated in the greenish mixture on the dead twigs, but fungal spores predominated in the blackish-green covering on the living twigs, especially on those infested with *Adelges*. Small amounts of lichen were also present, covering 6% of the upper surface of the 'dead twigs with *Pleurococcus*', 3% of the upper surface of the 'dead clean' twigs and less than 1% in the other two kinds of twig. On each of four days between 7 and 11 June 1956 twelve twigs of each type were taken from the same group of trees. Different groups of trees were sampled on different days, but these were all in a restricted area, approximately 60 yd in diameter at one end of this plantation. A total of 192 lengths of twig was taken, comprising 1200 cm of each of the four types. The numbers of individuals of each psocid species and of the possible predators present on each type of twig are given in Table 17, together with estimates of the total area in sq. cm of the *Pleurococcus*-fungal spore mixture and of the lichen of the forty-eight twigs of each type. In Fig. 5 the relative proportions on each type of twig, expressed as percentages of the total number on all the twigs, are presented graphically, for each *Mesopsocus* species and for the two species combined, with the corresponding distribution of the food for comparison. Both *Mesopsocus* species were in the second to fifth instar at this

period, the majority being third, fourth and fifth instar nymphs. The individuals of *Graphopsocus cruciatus* and *Cuneopalpus cyanops* were all fourth to sixth instar nymphs and those of *Reuterella helvimacula* and *Elipsocus hyalinus* were all adults.

The point of greatest interest in these results concerns the high population density of both *Mesopsocus* species coupled with the high degree of interspersion of their populations. Fig. 5 indicates that these animals were not aggregated on those twigs which carried the food, whose distribution was not, therefore, determining

Table 17. *Interspersion of psocid populations on larch trees at Harrogate, 7-11 June 1956*

Total numbers of individuals on forty-eight 25 cm lengths of twig (1200 cm) of each kind.

	Living twigs		Dead twigs		
	'clean'	'with *Pleuro-coccus*'	'with *Pleuro-coccus*'	'clean'	Total number
Mesopsocus immunis	93	154	89	102	438
M. unipunctatus	83	53	103	154	393
Total *Mesopsocus*	176	207	192	256	831
Cuneopalpus cyanops	7	4	0	0	11
Graphopsocus cruciatus	9	2	17	25	53
Reuterella helvimacula	0	0	27	3	30
Elipsocus hyalinus	0	0	1	2	3
Possible predators:					
Mite, *Anystis baccarum*	10	10	12	5	37
Spiders	1	2	2	0	5
Syrphid larvae	24	21	0	1	46
Lacewing larvae	0	0	2	0	2
Ladybird larvae	6	4	0	0	10
Empids	1	0	0	0	1
Cantharids	0	1	0	0	1
Area (sq. cm) of bark surface covered with: *Pleurococcus* and fungal spores	51	1134	1075	8	
Area (sq. cm) of bark surface covered with: lichen	7	11	81	44	

to any significant extent the distribution of the individuals of either species. This is also brought out clearly by the density of individuals on the dead clean twigs, on which the 256 individuals of both species are associated with 8 sq. cm of food-covered twig surface, *i.e.* 32 individuals, averaging 3 mm in length, per sq. cm of food. This is adequate for a few days' feeding only and indicates that such twigs are being used predominantly as resting sites. The relatively uniform spread of the total *Mesopsocus* population over the four twig types can be ascribed most simply to a tendency of individuals to move about at random when they are not feeding, but the possibility that the relatively high density promotes a spacing out of individuals cannot be excluded. The average *Mesopsocus* density over all the twigs sampled of 1 individual per 5·8 cm length of twig or 1 per 13 sq. cm of

twig surface, is similar to the lower density used in the experiments with *Mesopsocus* nymphs already described (Table 3), which demonstrated that increasing densities above this figure result in a greater spacing out of individuals.

Although the overlap of the populations of these two *Mesopsocus* species is extensive, it is not complete. The patterns of distribution of the two species (Table 17) are significantly different from each other ($\chi^2 = 59{\cdot}14$; $P < 0{\cdot}001$ with 3 degrees of freedom). Whether this difference is to be ascribed to differences between the species in their inherent preferences alone or is due to mutual interference between individuals of the two species cannot be decided from the data available. A test of association between the two species on a single type of twig

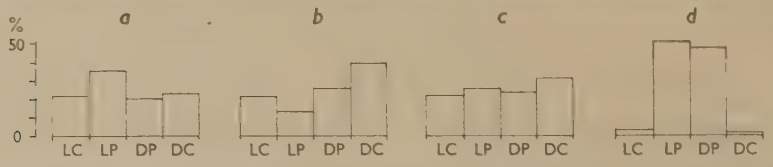

Fig. 5. Proportional distributions of the two *Mesopsocus* species and of their food over four types of larch twig, Harrogate, 7-11 June 1956. *a*, *Mesopsocus immunis*; *b*, *M. unipunctatus*; *c*, total *Mesopsocus*; d, food. L, living, D, dead twig; P, >80%, C, <4% of upper surface of twig covered with *Pleurococcus*-fungal spore mixture.

may, however, be carried out on the original data of the numbers of individuals of each species on the separate lengths of twig, by calculating the correlation coefficients for each of the sixteen groups of twig samples, each group comprising twelve twigs. All sixteen coefficients do not differ significantly from 0 at the 5% probability level. Within any one group of twelve similar twigs, therefore, the way *M. immunis* is scattered is uninfluenced by the presence of *M. unipunctatus* at the observed density, so that on any one twig type the populations of the two species would seem to be randomly interspersed.

The only point of interest regarding the other four psocid species present in these samples concerns the close correspondence between the numbers of the relatively sedentary lichenophilous species, *Reuterella helvimacula*, and the amount of lichen over the four types of twig. The distribution of the various predatory invertebrates (Table 17) suggests that the small, red, active mite, *Anystis baccarum* (L.) is an important psocid predator, since it is present in such large numbers on the dead twigs, upon which the psocids are virtually the only possible prey. Numbers of these mites have been captured with their psocid prey in this plantation at Harrogate, as well as the occasional spider, hemerobiid larva and harvestman. The almost complete restriction of the syrphid and coccinellid larvae to the living twigs suggests that these animals are preying chiefly upon the aphids and *Adelges*, but they may take some psocids as well.

DISCUSSION

This discussion will be restricted to the central theme of this paper, the coexistence of abundant species living in the same place and exploiting the same food resources. The almost complete restriction of the two lichenophilous species to

the lichen-covered portions of larch trees carrying both *Pleurococcus* and lichen (Tables 7, 13, 17) may be accounted for by the preferences demonstrated in the laboratory experiments (Tables 1, 2). Individuals of these species can, however, exploit *Pleurococcus* and fungal spores in nature, as the gut content analyses show (Table 4), but they are only able to do so when they form part of a population, most of which is maintaining itself on lichen. Where lichen is relatively scarce, as at Harrogate, these species are absent or present in very low numbers, although *Pleurococcus* is present in sufficient quantities to support large populations of the *Pleurococcus*-feeding species. Yet *Pleurococcus* is readily eaten by both lichenophilous species in the absence of lichen, without any deleterious effect on either mortality- or oviposition-rates (Fig. 1), and indeed the oviposition-rate of *Elipsocus mclachlani* is greater on *Pleurococcus* than it is on lichen. Whether the presence of the *Pleurococcus*-feeding species contributes to this inability of the two lichenophilous species to maintain populations in nature on *Pleurococcus* and fungal spores is at present not known. Although the two lichenophilous species live together on the same branches in several of the plantations studied, it appears likely that their populations have not yet reached a steady state there. The absence of *Reuterella helvimacula* in some of the plantations in which *Elipsocus mclachlani* occurs, owing to the restricted powers of dispersal of the former, suggests that *Reuterella* may be in process of colonizing other plantations where it is now present in only small numbers. The coexistence of these two species may therefore represent merely a transient stage before an equilibrium condition has been reached. The introduction of *R. helvimacula* into the Ha Mire plantation at Malham Tarn, which it has not yet reached and which supports the densest *Elipsocus mclachlani* population in this region of the Pennines, would be the most promising method of studying the interaction between these two lichenophilous species in nature, since climatic conditions at Malham appear to be ideally suitable for both of them.

The contention that two or more species with the same niche requirements cannot form mixed steady-state populations in the same region, which has been accepted by many ecologists, has recently been criticized by Andrewartha & Birch (1954). This contention is presumably intended to apply only to species occurring at high densities with respect to at least one of the niche requirements they have in common, since it is implied that competition will occur and will be sufficiently intense to result in the extinction of all but one of the species. No two species in nature ever have, of course, exactly the same niche requirements, and rarely, if ever, make exactly the same demand on one environmental resource. The work of Da Cunha, Dobzhansky & Sokoloff (1951) serves as a valuable reminder that, even where two species appear to feed upon the same foods, more critical investigation reveals quite subtle differences. Accordingly a study of interspecific competition in nature must be initially concerned with assessing the degree of similarity of the niche requirements of two or more species and with estimating the densities of the species with respect to these requirements. Interspecific competition may be said to occur when natality or mortality factors of one species are affected by the presence of another species in the habitat and by the

demands it makes upon some shared resource. Should such competition occur, its severity will be of prime importance, since fluctuating environments will allow only a limited time for its operation. Since mixed species populations under constant environmental conditions appear to be inherently unstable (Park 1954, 1955), the heterogeneity of natural environments both in space and in time may prove to be of the greatest importance in the understanding of how mixed species populations sharing a common resource are maintained in nature.

In these Pennine larch plantations seven common species, all dependent on the same food resources, *Pleurococcus* and fungal spores, maintain populations on the same trees. The presence of these species in so many of the plantations studied and their population levels at various altitudes suggest that each has had adequate time to colonize these woodlands and may be regarded as having reached equilibrium with respect to both the physical conditions and the presence of other species feeding on the same food. The seven species are very similar in size, in the way they graze their food, and in their life history, all stages of which are spent on the bark surface of the trunk and branches. Moreover since the nymphs and adults both eat the same food and live in the same place, each species population can be considered as a single ecological unit with regard to problems of grazing pressure and of population regulation.

To solve the problem how these mixed populations of psocids are maintained, it will be necessary to know whether food is ever scarce for long enough to affect differentially the populations of the species concerned, and if so whether compensatory factors then restore the balance, or whether this competition results in the local extinction of small subpopulations within a plantation, with subsequent re-establishment by immigration. The high absolute densities recorded give no indication of the likelihood of food shortage. There is no reason to suppose, for instance, that competition for food between the late summer species will be most intense in the hills, where population densities are highest, since climatic conditions there are probably the most suitable for rapid growth of the food organisms. Nevertheless, the density levels recorded, combined with the extensive removal of *Pleurococcus* from dead larch branches observed in the plantation at Harrogate, do suggest that local food shortages occur from time to time. The high degree of interspersion of the two *Mesopsocus* species in the early summer and of the four later summer species on the larch trees at Harrogate suggests that in such circumstances these populations will interfere with each other. It is also possible that the early summer populations of *Mesopsocus* influence appreciably the populations of the later summer species. Although the total late summer psocid population feeding on *Pleurococcus* and fungal spores increases in density with increasing altitude (Table 10), the early summer psocid population does not behave in this way. The total *Mesopsocus* population is in fact slightly more dense in the lowlands than in the hills, being 63·3 individuals per sample for the six localities at 300-550 ft above sea level and 49·9 per sample for the four localities above 900 ft (Table 8). Grazing pressure in the early summer, then, is somewhat greater in the lowland region, where a smaller total yearly amount of food is no

doubt available, than in the hills. This may contribute to the lower psocid population density in the lowlands later in the summer as compared with that at higher altitudes. The greater density of the early summer species (1·9 individuals per 10 cm length of twig) compared with the later summer ones (0·9 per 10 cm length) in the plantation at Harrogate is also worth mentioning here, although these estimates refer to different years. These early summer populations must certainly remove a considerable amount of food which would otherwise be available for the later summer species. The reverse influence is probably negligible, since the virtual absence of grazing during the winter months provides a respite for the food organisms.

When food is scarce, differential effects on the various species populations might result from differences in searching capacity combined with differences in the readiness with which they take the less nutritious foods such as bark flakes and detritus, and perhaps also from differences in their response to factors other than the abundance of food. In these larch plantations a reduction in the amount of food will be accompanied by an increased patchiness of its distribution, both over the twigs of one tree and over the trees in different parts of the plantation; this would give the more efficient searcher an advantage over the less efficient. The differences in behaviour between the two *Amphigerontia* species in the preference experiments illustrate both the differing readiness with which their nymphs take less nutritious food when their preferred foods are not available in the immediate vicinity, and their different searching capacities. Since oviposition-rates fall quickly when alternative and less nutritious foods are taken, decisive effects on future population trends could probably be produced by this means long before starvation point was reached. It has been shown by the experiments on *Elipsocus hyalinus* and *E. westwoodi* (Tables 15, 16) that these two species respond to factors other than the abundance of food, and these presumably play a part in determining the pattern of distribution over different kinds of twig on a single tree. Different responses by the different species to such factors may conceivably result in a larger proportion of the population of one than of another being present on food-covered twigs, thereby placing it in a favourable position at a time of food shortage. It would appear, for instance, from the distributions of the two *Elipsocus* species at Harrogate (Fig. 4) that *E. hyalinus* would be affected sooner than *E. westwoodi* should food become scarce, since a greater proportion of the former species is present on clean twigs. Although, however, the patterns of distribution of the three commonest species in this plantation at this time of the year, *Philotarsus picicornis*, *Amphigerontia bifasciata* and *Elipsocus westwoodi*, differ from each other, the proportion of the total capture from all twigs found on those carrying the food, was remarkably similar in each: 67·6% for *Philotarsus*, 64·7% for *Amphigerontia* and 71·6% for *Elipsocus westwoodi*. The corresponding figure for *E. hyalinus* is only 40·4%, but this species is believed to take lichen more readily than the others.

The two closely related species of *Mesopsocus* differ outstandingly in only one feature, the inability of *M. immunis* and the ability of *M. unipunctatus* to maintain populations above about 800 ft. In view of their great similarity not only in size

and body form but also in phenology and food preferences, the presence of these two species below this altitude together on the same twigs, and in some places as at Harrogate at high density and in almost equal numbers, is of great interest with regard to the problem of competition between allied species which require to share the same resources.

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SUMMARY

1. Nine psocid species make up over 95% of the psocid population on larch trees (*Larix decidua* Mill.) in the Pennine region of northern England and are the most important animals exploiting the microflora on the bark. This consists of lichen (*Lecanora conizaeoides* Cromb.), *Pleurococcus* sp. and fungal spores.

2. Feeding preferences and the effect of food upon oviposition-rates have been investigated by laboratory experiment. Seven species prefer *Pleurococcus* to lichen. When both these foods are available, little lichen is taken; when lichen only is presented, oviposition-rates fall and they gradually starve. Two species prefer lichen to *Pleurococcus*.

3. *Reuterella helvimaculata* eats the whole lichen. Mortality- and oviposition-rates on *Pleurococcus* are the same as on lichen.

4. *Elipsocus mclachlani* prefers lichen but feeds only on the apothecia; its oviposition-rate on *Pleurococcus* is greater than that on lichen.

5. The six *Pleurococcus*-preferring species feed mainly in nature on *Pleurococcus* and fungal spores.

6. Each species has the same habitat in all stages of its life history, and the nymphs eat the same foods as the adults.

7. The nine species fall into two phenological groups. The two *Mesopsocus* species overwinter as eggs, develop early in spring, become adult in June, and have only one generation a year. The others also overwinter as eggs but develop later, becoming adult in August and September; they also have one generation a year. Nymphs and adults of *Reuterella helvimaculata* and *Elipsocus hyalinus* can survive the winter in the lowlands, but not at higher altitudes.

8. *Mesopsocus unipunctatus* occurs at all altitudes, *M. immunis* only below 800 ft. *Elipsocus mclachlani* occurs only above 600 ft, and the remaining six species are present at all altitudes. Among the late summer species, the two lichen-feeders and the three commonest feeders on *Pleurococcus* and fungal spores all show denser population levels with increasing altitude.

9. In twenty-one of the twenty-four plantations sampled in late summer, two, three or four species feeding on *Pleurococcus* and fungal spores occur at moderate or high densities on the same trees at the same time; in five plantations three species live together at high densities even though *Mesopsocus* species are grazing these foods earlier in the season.

10. There has been adequate time for colonization of these larch plantations by all the species except *Reuterella helvimacula*.

11. The nine species studied include three groups of closely related species, but the members of each group differ in microhabitat. *Amphigerontia contaminata* predominates on living twigs, *A. bifasciata* on dead ones; *Elipsocus westwoodi* lives mainly on living branches, *E. melachlani* is almost restricted to dead ones, and *E. hyalinus* is intermediate; the two *Mesopsocus* species differ less and their populations overlap spatially.

12. Experiments with *Elipsocus westwoodi* and *E. hyalinus* confirm that factors other than abundance of food play a part in habitat selection. The distribution of the two lichenophilous species on a larch tree corresponds closely to that of their food.

13. For the late summer species the absolute densities at two highland and one lowland plantation were measured. At the highland localities the distribution of the various species closely followed that of their foods. The populations of the three *Pleurococcus*-feeding species were here highly interspersed at high densities. Average densities of 7·7 psocids per 10 cm of living twig and 5·9 per 10 cm of dead twig were found at Witton Fell. At the lowland locality the distributions of the four common *Pleurococcus*-feeders differ and show no close correspondence with that of their food; their populations overlap considerably.

14. In one lowland plantation two *Mesopsocus* species were present in almost equal numbers and averaged 1 individual per 5·8 cm length of twig. On twigs of any one type, these two species appear randomly interspersed.

15. The problems presented by the coexistence of these abundant species exploiting the same food at the same time are briefly discussed.

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A FIELD STUDY OF A POPULATION OF LEOPARD TOADS (*BUFO REGULARIS REGULARIS*)

By B. M. CHAPMAN and R. F. CHAPMAN

(With 10 Figures in the Text)

The studies to be described were made from April 1955 to March 1957 while we were living in the Rukwa Valley, south-west Tanganyika. This valley is a part of the rift valley system of East Africa and lies about 8° south of the equator at a height of some 2600 ft above sea level. All the observations were made at one place, Kafukola, a camp belonging to the International Red Locust Control Service, situated near the foot of the 3000 ft western escarpment. At Kafukola is a freshwater spring which has been dammed to form a pool about 15 × 25 sq. ft in area and some 2 ft deep at the centre. The pool has steep banks 1-2 ft high and is overhung by large fig trees whose roots extend into the pool in places. From the dam the water runs into a stream by the side of which is a banana grove. To the south of the pool the ground is largely cleared but on the other sides the grass is usually tall. Most of the observations on movement were made on the south side because of the difficulty of finding the toads in the tall grass elsewhere, and even here were restricted to the cleared area which extends about 100 yd from the pool. A brief description of the vegetation is given by Pielou (1952).

CLIMATE

Distinct wet and dry seasons are experienced in the Rukwa Valley, the wet season lasting from approximately November to April, the dry season for the remainder of the year. Virtually no rain falls during the dry season and under these conditions all other water supplies within about four miles of Kafukola may dry up. In the wet season, with an average rainfall of around 30 in., flooding of the plains of the valley floor is extensive and many rivers run down from the escarpment.

Screen temperatures usually reach 30° C or more each day, and only during January and February is the maximum temperature often less than this. The highest temperatures are recorded in October and November, just before the beginning of the rainy season. At this time daily maxima are generally above 35° C. Night minima are usually around 20° C but in July and August much cooler nights are common. The temperature of the water in the pool is always about 25° C, the constancy at all seasons being related to its origin at a spring.

The relative humidity is high during the wet season, regularly reaching 100% at night, but in the dry season falls to a low level with maxima generally not exceeding 50% and day-time values of about 20%. These figures are based on continuous records from a hygrograph in a standard meteorological screen.

The day length varies by about 55 min in the course of a year, the greatest length being in December and the shortest in June. Sunset is between 1715 and 1800 h (local time), depending on the time of year.

METHODS

The pool was visited after dark as frequently as was possible. At each visit all the toads seen were collected and marked by clipping their toes. This did not appear to have any ill-effects and healthy toads were frequently retaken some months after marking. After a time the clipped toes tended to regenerate and, though this was usually quite obvious, in such cases the toads were re-marked.

After marking, during which process they frequently voided water from the cloaca, each toad was weighed and measured and then released approximately where it had been captured. When a marked toad was recovered this fact was recorded; if more than a month had elapsed from the time it was last weighed, it was re-weighed and measured. Each month a few toads from each size-group were weighed and then dissected so that the development of the internal organs could be determined. Food in the stomach was identified as far as possible; fat bodies and ovaries were dissected out and weighed after the removal of excess moisture. The lengths of the testes and diameter of Bidder's organ were also recorded.

MOVEMENTS

During the dry season most of the amphibia in the Rukwa Valley aestivated, but *Bufo regularis* Reuss. was exceptional in that at least some individuals were active at all times of the year. It was likely that other individuals aestivated but no evidence of this was obtained.

Except during the wet season the toads were only seen at night. The day time was spent in secluded spots such as a hole at the foot of a wall, under half a brick or in a hole in the ground. In such situations the toads were protected from the extreme hazards of the climate as well as from possible predators. This was clearly of considerable importance in the hot dry conditions of the late dry season. At this time toads kept in cages without food died in a day or two if they were not given water, even though they were out of the sun in the coolest available situation in the laboratory. A toad in a hole 6 in. deep would experience lower temperature and higher relative humidities than it would at the surface of the ground so that its chances of death through desiccation would be considerably reduced.

Some measurements of temperature below the soil surface were made with thermocouples. At a depth of only 3 in. the maximum temperature recorded was 33·5° C while at the surface the temperature reached 47° C. These measurements were made in July; in November temperatures of up to 58° C were recorded. Although the thermocouples were in compressed soil it is apparent that air temperature in a hole 6 in. deep would be considerably less than at the soil surface and, especially in the hot season, this would be most important for the survival of the toads.

On a number of occasions marked toads were taken repeatedly in the same place

outside the pool, suggesting that they returned each day to the same hiding-place. Observations on other amphibia suggest that this is a frequent occurrence. According to Smith (1954) individuals of *B. bufo* L. return continuously to the same place, and in California Storer (1925) showed that *B. boreas* returned to the same shelter each day. The only other work on *B. regularis* showed that individuals of this species 'homed' overnight when displaced distances of up to $\frac{1}{4}$ mile (Jordan 1954).

Soon after nightfall toads were commonly seen and heard rustling through the grass. This movement was directed towards the pool as was indicated by the direction of movement and also from the recovery of marked toads. In all, seven toads were taken at distances up to 100 yd outside the pool and then again in the pool later the same evening, the two recoveries usually being made between 1800 and 2100 h. No suggestion was obtained of toads moving away from the pool early

Table 1. *Numbers of toads present in the pool at different times on the same evening*

	Time			
	1800	1900	2000	2100 h
22 January	1	2	4	–
22 May	–	–	16	18
24 ,,	–	–	10	11
25 ,,	3	5	24	18
28 ,,	–	–	12	19
3 June	–	–	10	11
4 ,,	–	–	5	7
5 ,,	–	–	12	12
7 ,,	–	–	7	5
8 ,,	–	4	13	–
14 ,,	–	–	7	7
28 July	–	3	7	–
13 September	–	7	11	–
17 ,,	–	–	11	5
20 October	–	8	17	–
21 November	–	3	5	–
10 December	4	8	11	–
17 ,,	–	3	6	–

in the evening, as might be expected if the movement was not specifically directed towards the pool. Visits to the pool in the late afternoon never revealed any toads except very occasionally during the breeding season when they were present all day. From Table 1 it can be seen that the number of toads in the pool rose sharply during the first two hours of darkness but then remained fairly steady or even fell off. This suggests that the toads became active in the early part of the night and took up to 2 h to reach the pool, but after this the movements were limited, the toads remaining in the pool until the early hours of the next morning.

Marked toads stayed in the pool once they had reached it and recoveries of individuals several times on the same evening were frequent. Occasionally toads remained in one place outside the pool for long periods, so that the nightly migration to the pool was apparently not invariable: this is also clearly indicated by the great seasonal variation in the numbers present. On one occasion a toad

taken in the pool at 2015 h was found 20 yd away from it at 2200 h. Thus the data on individual marked toads support the conclusions reached from the numbers present in the pool that a movement towards the pool in the early evening was followed by a period of relative quiescence during which the toads remained in the pool, later tending to disperse to their day-time hides. Toads did not always migrate to the pool and in such cases they were frequently found in damp situations, as where a flower garden had been watered in the evening. They were found pressed close to the moist soil in hollows and apparently stayed in these places for long periods. Particular toads were sometimes found in the same places on successive nights.

The stimuli resulting in the nightly movements of *B. regularis* may be separated into two groups, those causing the toads to become active, and those directing the movements towards the pool. The beginning of activity was clearly associated with nightfall, apart from those periods in which the sex drive was overriding, and at this time light intensity and air temperature were falling while the relative humidity was rising. Noble (1931) regarded the nocturnal activity of amphibia as being related to the higher humidity at night, and it is noteworthy that *B. regularis* was only active in the day time during the wet season. Even at this season, however, when humidity at ground level was extremely high all day, activity was much greater at night than during the day. This suggests that some factor other than humidity was important. It is difficult to separate the effects of temperature and light intensity. Both started to decrease about 2 h before sunset but the toads did not become active until later. However, the change from light to dark took only about 15 min and it was during this period that the first toads were seen on the move. At the same time toads kept in cages in the laboratory, where changes in temperature were not marked, also became very active. These toads only became active at other times of day during heavy rain showers accompanied by extremely poor light conditions. This evidence suggests that low light intensity was the stimulus promoting activity.

Apart from the sharp banks of the pool the ground sloped slightly upwards from east to west but from north to south there was no apparent slope. Most of the observed movements towards the pool were from the south so that these toads were travelling along the contours, and the movement could not have been directed by the slope of the ground. This conclusion was also reached by Savage (1935) working on *Rana temporaria* L. in Britain and Bogert (1947) showed that *Bufo terrestris* moved indiscriminately up and down slopes in homing experiments.

The number of toads visiting the pool was much lower in the wet season than when it was dry. This might be taken to indicate that a hydrotaxis was normally operative and that the toads were directed elsewhere during the wet season, but the fact that numbers of toads still visited the pool at times during the wet season, when large areas within 100 yd were deeply flooded and the ground all round was saturated, suggests that hydrotaxis was not important, since it could not operate under these conditions. Also Jordan (1954) observed that *B. regularis* homed to a dry veranda from a $\frac{1}{4}$ mile away and hydrotaxis could not be involved in this case.

This is true also in the return of toads to their day-time hides, this movement usually being away from water. Other workers (Breder, Breder & Redmond 1927, Savage 1935) have observed movement from one stretch of water to another, so that it seems clear that hydrotaxis cannot be important. Savage (1935) suggested that *Rana temporaria* might be directed to a particular pool by a specific pond smell. No data on this were obtained for *Bufo regularis*, but it is known that during the dry season the prevailing wind was from the south-east. Hence the toads moving to the pool from the south were moving approximately down-wind. This is not consistent with a reaction to an airborne smell. Moore (1954) also concluded that smell was not important in directing *B. bufo* since he observed movements towards a pool to be taking place from all sides on one night.

While making observations on movement it was observed that activity was induced by the croaking of toads already in the pool. Soon after croaking started movement would begin, ending again when it stopped. Movement was seen in the absence of croaking but there was no doubt that croaking did act as a stimulus. It was also noticed that as a general rule more toads were present in the pool when there was active croaking than when the toads were silent (Table 2). More

Table 2. *Numbers of toads present when croaking and when silent*

	Total observations	Number present (% observations)			
		1-5	6-10	11-15	16-20
Croaking	53	49	28	11	11
No croaking	49	80	18	2	0

than ten were present on 22% of the observations when the toads were croaking compared with only 2% when they were silent. Single toads were, however, frequently observed croaking, suggesting that the croaking was attracting more toads rather than that the toads were stimulated to croak by the presence of numbers of their fellows (but see p. 272). Thus it is possible that the toads were directed to the pool by the croaking of their fellows already present. If this was so it must be presumed that the arrival of the early ones was purely fortuitous, since none were present to direct them. This would not be difficult, since some spent the day in hiding quite close to the pool. However, Jordan (1954) observed *B. regularis* homing to his veranda. It is most unlikely that any toads remaining on his veranda were calling, although this was not recorded, so that, in this case at least, some other factor must have been involved. Working on other species of amphibian, Bogert (1947) suggested that croaking guided distant individuals to their home locality, but Savage (1935) and Moore (1954) did not consider voice important in this respect. Bogert (1947) believed that his frogs homed by visual means when they were in familiar territory and this has also been suggested by Moore (1954). Since *B. regularis* was mainly nocturnal it is difficult to see how the toads could have been directed visually, but it does seem possible that they might have had a knowledge of their home locality. By this is meant a learnt visual, olfactory and tactile knowledge of the area by which the toad was able to find its way about.

This would also account for the ability of the toads to find their way back to their day-time hides, which movement was no less directed than the move towards water. Thus it appears likely that in its nightly movements *B. regularis* was able to find its way to and from the pool as a result of its general familiarity with the area, while later arrivals were certainly stimulated to move and possibly also guided by the calls of their fellows.

The greater distances which the toads moved to the pool are not known. Some spent the day in holes in the tree roots adjacent to the pool and others were found in hiding up to 100 yd away. Toads marked and released 100 yd from the pool were later recovered in it, but none was released at greater distances. Jordan (1954) recorded homing in *B. regularis* from $\frac{1}{4}$ mile away and distances of up to $\frac{3}{4}$ mile in one night have been recorded for other species (*e.g.* Breder *et al.* 1927, Bogert 1947, Moore 1954).

Particular toads occupied the same positions in the pool night after night and would return to their posts within a few minutes of being released in other parts of the pool. Thus, one large male was recovered fifty-three times and it was nearly always in one of two positions, either under a particular tree root or in a cavity in the dam. Most of the regular visitors to the pool had particular stations which they always occupied, usually in places with easy access to cover in case of attack. The ability to find their way back quickly to these stations suggests that the toads had an intimate knowledge of the pool.

In a total of thirty marked toads recovered more than ten times each in or near the pool fifteen were mature males, having well-developed digital pads, and the remainder were immature males or females. This shows that the movements to the pool were not only associated with breeding activity.

NUMBERS VISITING THE POOL EACH NIGHT

Since the number of toads present in the pool increased for the first two hours after dark, in this section, which deals with the variation in the number of visitors from night to night, only observations made between 2000 and 2100 h, when numbers were usually maximal, are considered. The number present varied considerably from night to night and throughout the seasons and Fig. 1 gives the monthly averages for the period of the observations. Very large numbers of toads were present in May and June 1955 but apart from this the general trends were similar in the two seasons. The number tended to increase as the year progressed until a maximum was reached in November. This was followed by a very sharp fall and only very small numbers of toads visited the pool from December to March.

The very low numbers were found in the rainy season and the sharp drop in numbers followed immediately after the first heavy rains of each season although these day to day variations cannot be shown in the figure. The gradual rise after the rainy season, continuing until the beginning of the next rains, was associated with conditions becoming progressively drier and hotter. It is probable that the numbers present at different times may be directly related to these conditions.

As the season progressed and more and more of the water remaining from the floods of the previous rains dried up, larger numbers of toads came to the pool at Kafukola because their previous living area became too dry and uninhabitable. At the beginning of the rains large areas became flooded again and the toads scattered, relatively few now visiting the pool. This state of affairs persisted throughout the rainy season, the number of visitors to the pool increasing again as the floods receded.

The marked difference between May and June 1955 and the same months in 1956 may be attributed to similar causes. In 1955 the rains ended somewhat

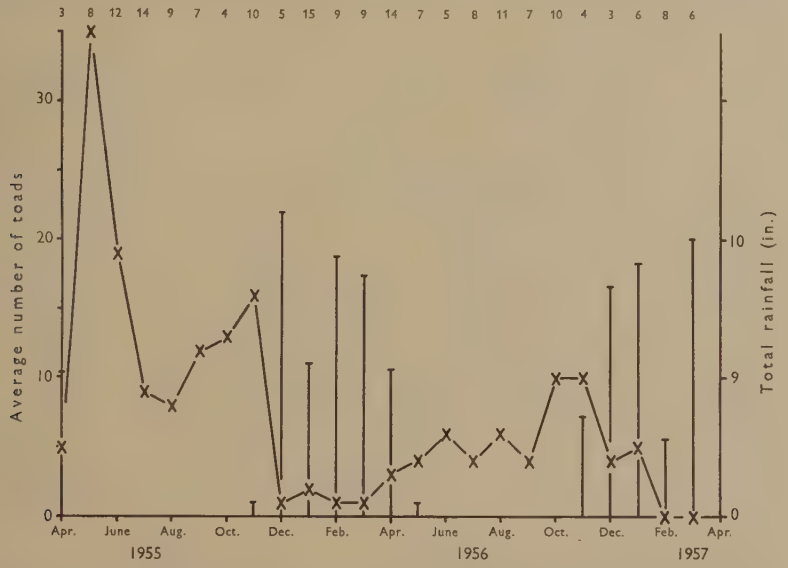

Fig. 1. The average numbers of toads visiting the pool during the period of the observations and the total rainfall for each month. Figures along the top show the number of counts on which each point is based.

abruptly and there was very little flooding. This could account for the large numbers of toads present at the pool in May. In 1956 flooding was extensive and persisted for a long while so that there was no rapid congregation at the pool. The difference in wetness between the two years might also account for the generally larger number of visitors to the pool in 1955, the drier year. In 1956 more suitable localities remained at all times so that the population was spread over a larger area.

The reason for the decline in numbers in June and July 1955 is not clear. It is probable that some *B. regularis* do aestivate during the dry season, and the reduction may have been connected with this habit; or perhaps the very large number of visitors became depleted through predation, attracting attention to themselves by their frequency.

There were marked fluctuations from night to night in the numbers of toads visiting the pool, quite apart from the seasonal variations. In order to study this the period from April to September 1956 only was considered, as during this time no major seasonal fluctuations occurred although the number present on any one night varied from 0 to 13.

Many authors have regarded rain as being important in the migration of amphibia (Blanchard 1930, Bogert 1947, Moore 1954) but during the period under consideration there was no rain after the first two months although the toads continued to visit the pool. Rain can, therefore, be discounted in the case of *B. regularis*. Nor was there any correlation between the number of toads present and the relative humidity either of the day preceding or of the night in question. There was no association between the number of visiting toads and the temperature. The correlation coefficients of the numbers with the previous maximum and minimum temperatures and with the temperature at the time of the observations were worked out, but in every case the coefficient was very low and not significant statistically. In addition, the phase of the moon, cloudiness, and darkness of the night were also considered in relation to the number of toads in the pool. Since activity was only observed in darkness, it was thought possible that movement might be reduced on moonlit nights, in which case activity would have been at its maximum around new moon. This was not so, nor was there any relationship with the darkness or cloudiness of the evening, darkness being a function of the phase of the moon and the amount of cloud, which was estimated subjectively. Chi squared tests were used to find the significance of these relationships.

Thus, no evidence was obtained to suggest that the variation in the number of toads visiting the pool was in any way influenced by the external conditions. Possibly the state of hunger or desiccation of the toads themselves was important.

CROAKING

Only toads in the pool were heard to croak except for very occasional instances in the wet season. Hence, again with the exception of the wet season, this was a nocturnal activity. Hewitt & Power (1913) said that both sexes called, the female replying to the male, but at Kafukola only mature males with pads were seen calling. The voice of the female as described by Hewitt & Power resembled the cry made by males seen to be mounted in error by other males and it may be that confusion arose because of this. The offending male immediately released its partner following the call, which was thus apparently important in sex recognition. Savage (1934) described a similar call used for sex recognition in *B. bufo*.

Isolated toads did call but when greater numbers were present one individual calling would stimulate others to do the same. The first arrival at the pool would croak spasmodically at intervals of 5-10 min until a second toad joined in, when croaking persisted for about 30 sec at each burst. As more toads arrived calling became more frequent, periods of croaking of 1 min or so being separated by quiet periods of about 2 min. When large numbers were present croaking was sometimes more or less incessant. Loveridge (1953) gives an instance of *B. regularis* croaking

in response to the crackling of a bush fire and Noble (1931) records that calling was mutually stimulated in other amphibia.

The voice of *B. regularis* was used to attract females, for the males did not go in search of mates but took up calling stations in shallow water all round the edge of the pool, as was also observed by Hewitt & Power (1913). The calling stations of individual toads were well separated and croaking toads were never seen within about 1 yd of each other. In this way the males were able to attract females to themselves in the same manner as *B. bufo* (Savage 1934).

Although *B. regularis* was heard calling at all times of year, the toads did not always call whenever they were present in the pool. Only mature males were seen calling so that in their absence croaking was not heard, but even when mature males were known to be present they did not necessarily croak. More toads were present when the males were calling but up to nine, including mature males, were observed to remain silent. There were too few cases in which mature males were known to be present but not calling to make statistical analysis of any value in determining the factors influencing calling, but inspection of the data did not reveal any obvious effect of the external environmental factors. Moore (1954) found that the calling of *B. bufo* was affected by temperature but no comparable influence was observed with *B. regularis*. Noble (1931) said that high humidity was important, calling being induced by sharp increases in humidity, but, while it is true that *B. regularis* only called when in very moist situations, it is equally true that they often did not call when in these situations. There was no correlation of calling with relative humidity, as recorded in the adjacent Stevenson screen, but in any case the relationship between records made in the screen and the levels of humidity to which the toads at the edge of the pool were subjected must have been extremely remote.

Calling stopped when the pool was suddenly illuminated by a lamp but was resumed if no further disturbance occurred. It is probable that the initial stopping was related to the sharp change in stimulation rather than the presence of the light itself. Croaking was only heard in the day time when spawning was taking place, the sex drive presumably being very high at this time so that other reactions, normally resulting in the retreat to a hide during the day, were suppressed.

BREEDING

Egg-laying occurred mainly during the rainy season from November to January but a few pairs were observed to breed in August or September. This occurred in both 1955 and 1956. Loveridge (1953) also apparently observed this pattern in Nyasaland since he recorded spawn in July and August and tadpoles in August and from November to January. The rainy season in Nyasaland is similarly distributed in time to that in the Rukwa. Hewitt & Power (1913), Power (1927) and Rose (1950) also observed the breeding of *B. regularis* to occur during the rainy season.

It was hoped that the anomalous breeding outside the main breeding season might give some key to the factors controlling it. In mid-September 1955 three

females spawned, the spawning being preceded by an increase in the number of toads visiting the pool and a great deal of croaking. During this period the relative humidity showed a slight increase compared with the previous weeks; the maximum was between 70 and 80% compared with 60-70% and the minimum 30-40% instead of 20-30%. Very high winds were common at this time and on one night, when spawning occurred, a distinct smell of rain was detected. It apparently rained on the escarpment some distance away. This suggests that breeding was associated with an increase in relative humidity. Spawning was also observed in the middle of August 1956 but in this case the weather was quite normal for the time of year. No increase in relative humidity was recorded, the minimum being regularly at about 20% and the maximum 70-80%, while the skies remained quite cloudless for the few days immediately before and after the spawning.

Males with digital pads were obtained at all times of year and croaking was also heard in every month. Clasping was observed, either in the pool or in cages, in all months except February and March, the months immediately following the main breeding season. Smith (1938) stated that the development of the clasping reflex in *Rana* was related to the secretion of testicular hormone, so it is justifiable to regard the tendency of males to clasp as an indication of their sexual maturity. Hence the combined evidence of digital pads, calling and clasping suggests that, with the possible exception of the months of February and March, some males of *Bufo regularis* were capable of breeding at all times of year. Thus it is probable that the time and frequency of spawning was limited by the incidence of mature females. There were two possible ways in which the incidence of mature females at the pool could be varied. Either they were only mature at certain times of year or they were mature throughout the year but only came to the pool at certain times. The fact that spawning occurred in August 1956 in the absence of any obvious external stimulus suggests that females visited the pool whenever they were mature, irrespective of the external conditions. Thus it is probable that, with a few exceptions, females only matured during the rainy season.

When they were close to the pool females were attracted by the calls of the males round the edge. As a female approached a male the latter would sometimes advance a short distance out of the water to meet her. Mounting followed at once and usually occurred at about 2000 h. The toads remained *in amplexu* until after the female had spawned next morning but they were never seen to remain paired for longer than this. Spawning was not obviously influenced by the external conditions. It occurred after wet and dry days with equal frequency and was not related to the overnight relative humidity or temperature. Savage (1935) was similarly unable to relate spawning in *Rana temporaria* to the external conditions and it may be that the development of the gonads was more important.

Oviposition took place at about 0700 or 0800 h in the morning, the pairs remaining *in amplexu* overnight without spawning. Pairs were very wary, except while they were actually spawning, and often swam into deep water on being approached. Unpaired toads were less nervous and were rarely seen in the deep water in the middle of the pool even though the water was quite clear so that they would have

been readily visible. The time lag between mounting and spawning may have been necessary for the sex drives of the male and female to become synchronized, while oviposition could have been triggered off by the high light intensity or rising air temperature, since the paired toads remained partly out of the water at the edge of the pool.

Spawn emission and ejaculation by the male, as indicated by its pumping movements, were followed by a few minutes of inactivity. After this the female shifted its position, the egg strings becoming stretched out as a result, and then spawn emission was repeated. Each emission of spawn lasted only 10-20 sec while successive emissions occurred at about 3 min intervals and the whole process of spawning was completed in little more than an hour. Savage (1934) recorded that in *Bufo bufo* the interval between successive emissions was about half an hour and spawning occupied several hours. This marked time difference may be related to temperature differences since the temperature of the water at Kafukola was about 25° C while in Britain *B. bufo* breeds in water only a little above freezing.

The spawn was laid in shallow water 1-2 in. deep all round the edge of the pool wherever there was a suitable site. There was no selection of a particular spawning site such as Savage (1934) recorded for *Rana temporaria*. The only other toad which frequented the pool was *Bufo carens* and the eggs of the two species were readily separable by their size. One hundred and eighty eggs from eighteen different strings of *B. regularis* were measured immediately after laying and all had a diameter between 1·0 and 1·5 mm. Hewitt & Power (1913) gave the size as 1·5 mm and Power (1927) as 1·0 mm. The eggs of *B. carens* were much larger and Power (1925) gave the diameter of the eggs as 2·5 mm. Long strings of eggs were laid in the shallow water, parallel with the edge. Each female moved for a distance of about 4 ft around the edge of the pool laying eggs and then doubled back on her tracks so that several strands of spawn were laid along a limited stretch of the bottom of the pool. Large numbers of eggs were laid by each female and estimates of over 20 000 were given for this species by Power (1927) and Rose (1950).

The tadpoles hatched in two days and after four days were 6·5 mm long with large external gills. No attempt was made to follow the life-history through in Rukwa, but large tadpoles nearly ready to metamorphose were recorded in April 1956, 51 days after the last spawning, in October 1956, 73 days after spawning, and in March 1957, 56 days after spawning. These figures are similar to those given by Power (1927) who recorded a minimum time from hatching to metamorphosis of 73 days.

GROWTH

Although the very largest specimens were females, there was in general no marked difference in size between the sexes. Hence the data for the two sexes have been pooled except where one sex is specifically referred to. Table 3 shows the relationship between length and weight for the month of May. Similar data were obtained for each month but the results are not combined as the increase of weight with length was found to be variable. Fig. 2 shows the seasonal change in

the average weight of toads in three specified length-groups, the data for December to March being combined because of the paucity of observations in these months. From March to May toads of a given length were increasing in weight but after

Table 3. *The relationship between weight and length for the month of May*

Figures show the percentage of each weight in the given length-group.

Weight (g)	Length (mm) 30-34	35-39	40-44	45-49	50-54	55-59	60-64	65-69	70-74	75-79	80-84	85-89
Number in sample	2	2	5	14	43	63	53	25	14	7	4	2
0-4	**100**	**100**	.	.	.	.	.	.	.	.	.	
5-9	.	.	**100**	29	2	.	.	.	.	.	.	
10-14	.	.	.	**71**	**67**	8	2	.	.	.	.	
15-19	.	.	.	.	28	**73**	17	.	.	.	.	
20-24	.	.	.	.	.	19	**49**	16	7	.	.	
25-29	.	.	.	.	2	.	30	**52**	29	.	.	
30-34	.	.	.	.	.	.	2	24	14	.	.	
35-39	.	.	.	.	.	.	.	8	29	29	.	
40-44	.	.	.	.	.	.	.	.	14	**43**	.	
45-49	.	.	.	.	.	.	.	.	7	14	25	
50-54	.	.	.	.	.	.	.	.	.	14	**50**	
55-59	.	.	.	.	.	.	.	.	.	.	.	
60-64	.	.	.	.	.	.	.	.	.	.	25	
65-69	.	.	.	.	.	.	.	.	.	.	.	
70-74	.	.	.	.	.	.	.	.	.	.	.	50
90-94	.	.	.	.	.	.	.	.	.	.	.	50

this they tended to become lighter until the latter part of the year when there was an indication of a further increase in weight.

The variation in weight for a given length was related to the season. The toads increased in weight when it was wet and decreased when it was dry. This may have been related to the greater abundance of food in the wet season and also to

Fig. 2. The seasonal change in the mean weight of toads in a given length-group.

increased water loss in the dry period. The importance of this last factor was indicated by the fact that two toads kept in dry cages in June lost 5% of their weight overnight and in these conditions toads died within a few days. Others in

identical cages but supplied with water remained quite healthy. Ott (1924) showed that, because of the absorption of water, *Rana pipiens* Shreber kept in cool water did not show any progressive loss in weight even when starved, but at temperatures around 20° C the loss in weight was rapid. Thus desiccation and the absorption of water play a very great part in determining the weights of amphibia. These changes in the amounts of available food and water were also reflected in the growth of individual toads. From the repeated recovery of marked toads it was possible to follow the growth of individuals and some examples for the

Fig. 3. Seasonal changes in the weights of individual toads.

different seasons are given in Fig. 3. Growth occurred mainly during the period November to June while for the remainder of the year most individuals tended to lose weight.

The size make-up of the population taken as a whole showed marked seasonal changes. Fig. 4 shows the most abundant size-group obtained in the samples for each month of the year, the figures for the whole period of the observations being combined. In this figure the weights of the toads are used but an essentially similar result could be obtained by using the lengths. In February and March most of the toads were very small, having only just metamorphosed, but in the next two months progressively larger toads became the most common because of the rapid growth which was occurring. From May to September the size make-up of the population remained constant because of the period of reduced or retrogressive growth observed in individuals. After September the toads started to grow again so that the weight of the commonest size-group increased. The sharp drop from January to February was due to the appearance of large numbers of newly metamorphosed toads for the first time.

Fig. 3 suggests that smaller toads grew more rapidly than older ones and the data are presented fully in Table 4. This shows the much faster relative increase in weight of small toads in the growing seasons, while the loss at other times was similar in all the size-groups. The seasonal change in growth is also apparent.

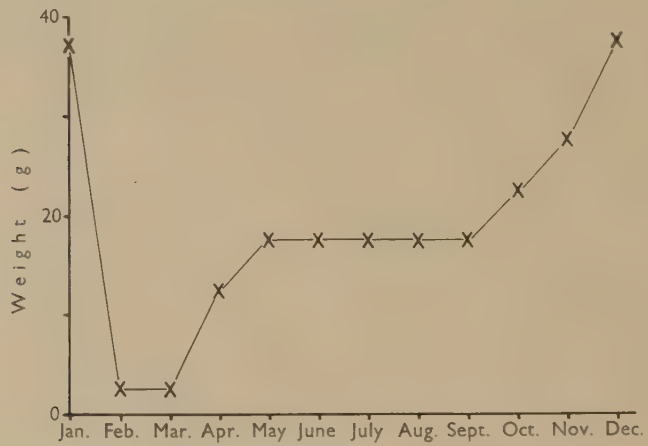

Fig. 4. The most abundant size-group in the population at different seasons.

Mature, gravid females were found to be markedly heavier, length for length, than other members of the population at the same time of year. Fig. 5 gives the

Table 4. *The relative changes in weight of different sized toads at various times of year*

Figures give the percentage change in weight with the number of observations in parentheses.

	Weight (g)		
	0-19	20-39	40-59
January	–	3 (2)	1 (2)
February	–	13 (1)	−1 (2)
March	–	–	6 (1)
April	–	–	0 (1)
May	25 (6)	5 (4)	0 (4)
June	30 (23)	16 (50)	7 (8)
July	7 (13)	−1 (22)	−2 (4)
August	−5 (12)	3 (18)	1 (6)
September	−4 (9)	−4 (17)	−7 (4)
October	0 (4)	3 (10)	3 (4)
November	32 (4)	8 (25)	7 (11)
December	–	1 (4)	4 (1)

live weights and lengths of females dissected in October, November and December and shows that the weight of a female may be increased by about 20 g by full development of the eggs. March (1937a) obtained similar figures for *R. temporaria*.

FOOD

The food of *Bufo regularis*, as ascertained by the examination of stomach contents, consisted almost entirely of insects (Table 5) and in most cases included beetles. Power (1937) dissected thirty *B. regularis* and also concluded that insects formed the bulk of the diet, 85% consisting of various species of grasshopper. It is probable that the toads fed on whatever happened to be available. Thus one

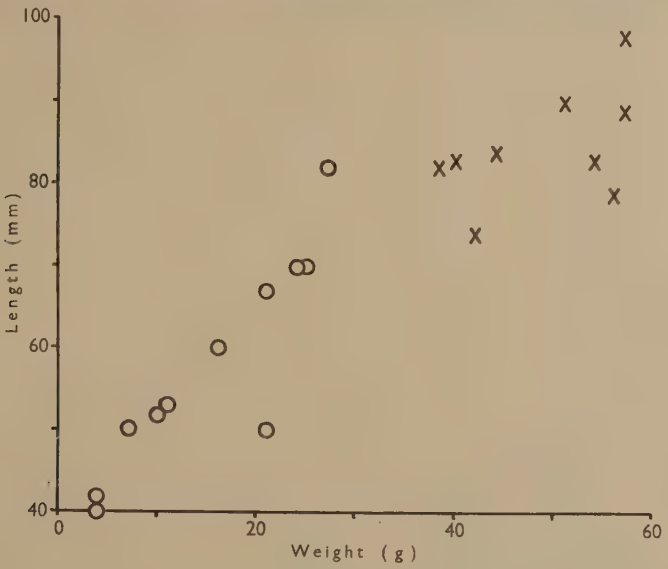

Fig. 5. The relation of weight to length in female toads with well-developed (X) and poorly developed (O) ovaries. Data for October to December.

specimen was found to have eaten 135 *Musca* sp. and others were seen feeding freely on termites as the winged forms emerged from their nests at the beginning of the rainy season. Aquatic beetles and bugs were sometimes taken but the insects in the stomachs were not usually associated with any one particular habitat, and it appeared that the toads fed whenever and wherever they were able.

Table 5. *Food found in the stomachs of* Bufo regularis

Total no. examined	Number containing				
	Coleoptera	ants	Hemiptera	other insects	spiders
85	65	36	16	19	1

FAT

Bufo regularis has a large, branched, yellow fat body which at its greatest development formed about 5% of the total body weight. The relative size of the fat body was not related to the size of the toads but it did show marked seasonal

variations in development (Fig. 6). In males the size of the fat body is expressed as a percentage of the total body weight, but in females it is given as a percentage of the residual body weight after subtraction of the weight of the ovaries. In both sexes the fat bodies increased in size from March to June. After this there was a steady decline until in November the fat was barely visible and it remained in this reduced state until March. The fat bodies of the two sexes were similar in

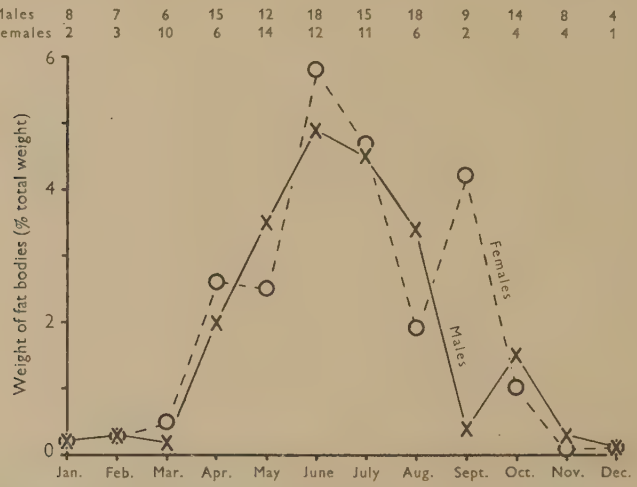
Males 8 7 6 15 12 18 15 18 9 14 8 4
Females 2 3 10 6 14 12 11 6 2 4 4 1
Weight of fat bodies (% total weight)
0
2
4
6
Jan. Feb. Mar. Apr. May June July Aug. Sept. Oct. Nov. Dec.
Males
Females

Fig. 6. Changes in the weight of the fat bodies. In this and the following figures the sizes of the various organs are expressed as percentages of the total weight or length of the toads. The numbers at the top show the number of toads on which each point is based.

size at all times. Ott (1924) found that the fat body in male *Rana pipiens* was much larger than in females but it only amounted to about 1% of the total body weight. On the other hand Kennel (1912) found that the fat body in an unspecified species of frog was much greater in the female than in the male at the time of greatest development.

In *Bufo regularis* the fat was stored when food was plentiful. The subsequent reduction was similar in both sexes and occurred over the dry season, well before spawning, suggesting that the fat was utilized as a somatic reserve, tiding the toads over the arduous period of the dry season. However, the state of the fat bodies in females was related to the development of the ovaries (Fig. 7). Very few females containing well-developed eggs were examined, but in those that were the fat bodies were extremely small. Large fat bodies were always associated with poorly developed ovaries. This suggests that the fat may have provided nourishment for the developing gonads in addition to its somatic function. Work on other amphibia also leads to this conclusion. Kennel (1912), having shown that the gonads developed normally after extirpation of the fat bodies, concluded that

'les corps adipolymphoïdes ont une fonction de réserve somatique'. On the other hand, Adams & Rae (1929) found that the fat bodies were essential for the development of the gonads of *Triturus viridescens* (Raf.) since the gonads degenerated after their removal even if the animals were fed; they had no evidence of the effect of the fat bodies on organs other than the gonads. Finally Ott (1924) showed that the fat did provide an important somatic reserve in *Rana pipiens*. When the frogs were starved for long periods there was no loss in the total weight

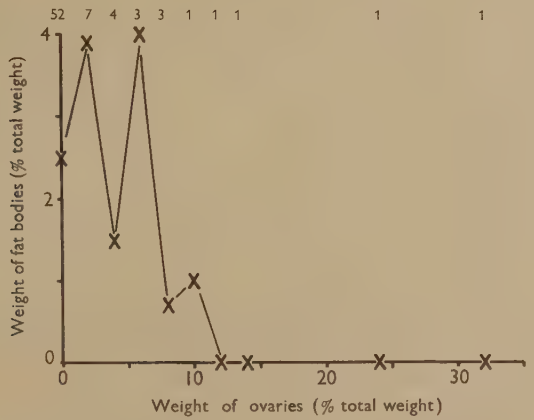

Fig. 7. The size of the fat bodies in relation to the development of the ovaries.

until the weight of the fat bodies was reduced by 77%, the weight of the body as a whole being maintained at the expense of the fat. This laboratory evidence thus supports the conclusions reached in the field study of *Bufo regularis* that the fat bodies provide a reserve of food for the gonads and also for the body as a whole.

GONADS

In mature males of *B. regularis*, 60 mm or more from nose to vent, the length of the testes was about 20% of the total body length. No testes were found in toads less than 30 mm long, and in toads less than 40 mm long their length was only about 15% of the length of the toads. They thus showed slight positive allometry in their growth as was also observed by March (1937a) in *Rana temporaria*.

Fig. 8 shows the seasonal variation in the lengths of the testes. Only toads over 60 mm long are considered in order to eliminate the effects of allometry as far as possible. Maximum development was reached in the breeding season and the minimum just after it, in March and April. Thus, although some males appeared to be in breeding condition at all times of the year (p. 274), there was an annual cycle in the development of testes in the population as a whole. March (1937) recorded that the testes of *R. temporaria* were heaviest just before breeding.

In the field males were judged to be mature when they had developed digital pads. In general, males over 25 g in weight were found to be mature, but as the breeding season approached smaller individuals developed pads (Table 6). Comparing Table 6 with Fig. 3 it appears that the toads may have come into breeding condition in their first season when little more than six months old.

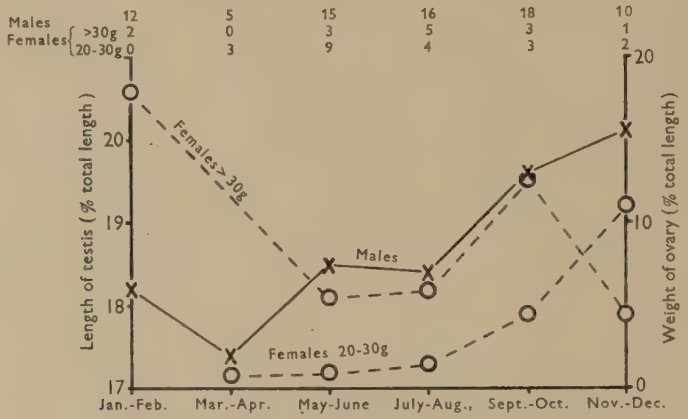

Fig. 8. Seasonal changes in the development of the gonads.

Ovaries were not found in toads less than 25 mm long. When present, each ovary was found to have from eleven to twenty-nine lobes, with an average of nineteen from seventy-four females. These numbers include small secondary lobes cut off from the main ones. The number of lobes did not vary with age but their size increased as the eggs became larger. Lobes containing fully developed eggs

Table 6. *The percentage of males in different size-groups having digital pads at the various seasons*

Numbers of observations in parentheses.

Weight (g)	Jan.-Feb.	March-Apr.	May-June	July-Aug.	Sept.-Oct.	Nov.-Dec.
0-9	0 (1)	0 (7)	0 (12)	0 (8)	–	–
10-19	50 (2)	0 (10)	0 (12)	0 (10)	46 (13)	100 (3)
20-29	100 (6)	0 (1)	0 (5)	57 (7)	94 (32)	100 (12)
30-39	100 (17)	75 (4)	100 (4)	37 (8)	100 (21)	95 (22)
40-49	100 (11)	80 (5)	100 (9)	100 (3)	100 (4)	100 (12)
50-59	100 (2)	100 (1)	100 (3)	100 (2)	100 (1)	100 (2)

were 15 to 20 mm long. The total weight of the ovary also increased with egg size (Fig. 9) As the eggs became larger their appearance altered. At first they were transparent with readily visible nuclei, then they became opaque and pigmented, and finally, as the yolk was deposited, bipolar. As with the testes in the males, the development of the ovaries in the females varied with the season.

In old females over 30 g the weight of the ovary fell after breeding and rose again in October at the beginning of the next rainy season (Fig. 8). The low figure for December arose from a single individual which had eggs already in the body cavity so that the relative weight of the ovary was reduced. In smaller toads, 20-30 g, in their first year the ovaries developed rapidly and they were capable of breeding in their first rainy season (Fig. 8).

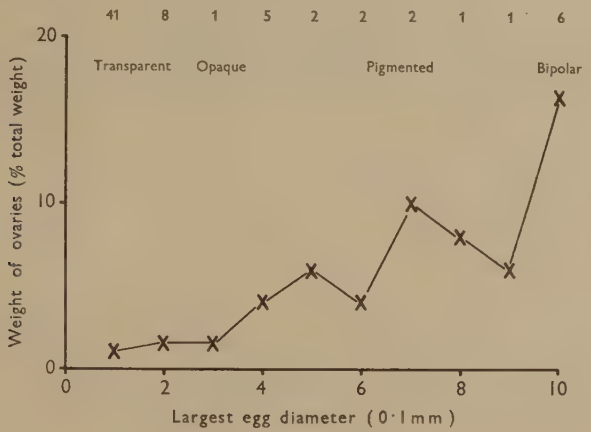

Fig. 9. The changes in the weight of the ovary relative to the size of the developing eggs.

Hence, although breeding did occur at other times of year, there was a marked seasonal cycle in the gonadial development of both sexes, reaching a peak in the first half of the rains, from November to January. March (1937b) showed that the development of the gonads was controlled by a secretion from the anterior pituitary but the factors influencing this organ are unknown. It was possible that the development of the gonads in *Bufo regularis* was influenced by the rainy season but toads did breed outside the rainy season, and nearly all showed advanced development of the gonads well before the rains started. There was no marked rise in humidity before the rains but they were preceded by a period of extremely high temperatures with daily maxima usually exceeding 35° C. In 1955 temperatures were much higher than in 1956 but the main spawning was two weeks later, coinciding with the beginning of the rainy season. Savage (1935) showed that the spawning date of *Rana temporaria* was related to previous temperature and the wetness of the area, and it may be that the ovarian development of *Bufo regularis* was influenced by temperature but that spawning was delayed until the rainy season. Finally, it is possible that the development of the gonads was related to changes in day length. It is known that animals living close to the equator are influenced in this way. At the time of gonadial development day length was increasing. Further light might be thrown on this by a study of some of the amphibia which aestivate over the dry season. These frogs and toads breed at the

same time as *B. regularis* but it seems very unlikely that they could be influenced by changing day length since at least some spend the dry season buried in the soil, emerging only at the beginning of the rains.

BIDDER'S ORGAN

Bidder's organ was present in both sexes of *B. regularis*, its greatest diameter being about one quarter of the length of the testis in the male and of comparable size in the female. De Vos (1935) found that Bidder's organ persisted in the males of *B. regularis* but disappeared in large, mature females. In the Rukwa toads Bidder's organ was reduced in mature individuals of both sexes (Fig. 10).

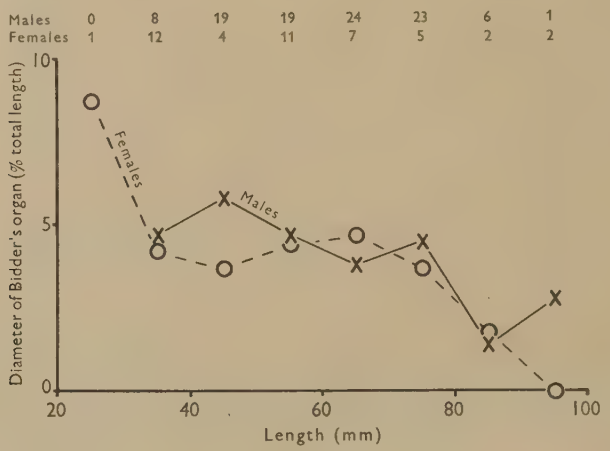

Fig. 10. The size of Bidder's organ in relation to the size of the toads.

A total of eight out of 118 males were found to have atypical testes, which were associated in some cases with the loss of the normal Bidder's organ. This figure is not excessive; Witschi (1933) found that about 20% of the males in a sample of 3300 *B. bufo* had atypical testes.

ACKNOWLEDGMENT

We are indebted to Dr A. Loveridge for identifying the toad.

SUMMARY

1. An ecological study of the leopard toad, *B. regularis*, was made in the Rukwa Valley, Tanganyika Territory. Movement and growth were studied by marking and recovery and monthly samples were dissected.

2. There was a nightly movement of toads to and from the pool, the days being spent in hiding. Movement began soon after nightfall and appeared to be stimulated by the low light intensity. Toads were able to find their way to the pool as a

result of their general familiarity with the area, but they were also guided by the calls of their fellows already in the water.

3. Apart from nightly fluctuations, the number of toads in the pool increased as the dry season advanced but fell sharply as soon as the rains began, remaining low so long as the rains lasted. These changes were related to the availability of water elsewhere than in the pool.

4. Oviposition occurred mainly from November to January, during the rainy season. Some males were mature at all times of year. Egg-laying was seen only in the mornings in shallow water all round the edge of the pool.

5. Growth was mainly during and after the rainy season when food was abundant and desiccation at a minimum. Small toads grew faster than large ones. The food consisted almost entirely of insects.

6. The fat bodies constituted at their maximum about 5% of the total body weight. Their development was seasonal, reaching a maximum in June.

7. Growth of the testes was allometric and even in old males there was seasonal variation in size. The greatest development was reached during the rainy season. Males matured in their first year.

8. The ovaries each contained an average of nineteen lobes which increased in size as the eggs developed. Development was maximal during the rains and may have been associated with high temperatures or with increasing day length.

9. Bidder's organ was present in both sexes but was reduced or absent in old individuals.

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OBSERVATIONS ON THE GROWTH OF PERCH (*PERCA FLUVIATILIS* L.) OVER TWENTY-TWO YEARS WITH SPECIAL REFERENCE TO THE EFFECTS OF TEMPERATURE AND CHANGES IN POPULATION DENSITY

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(With 17 Figures in the Text)

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INTRODUCTION

The size of fish in a population depends both on factors which affect the average age of the fish and on factors which affect the growth-rate. The growth of fish has therefore been the subject of considerable study, particularly by means of the size-for-age analysis of samples of fish taken from different populations at different times or localities. Experimental studies on various aspects of growth have been carried out on fish in laboratory aquaria and ponds, but comparatively few experiments have been made on the effects of changing conditions on fish in their natural environment.

When Worthington (1949) started an experimental fishery on Windermere with the object of effecting substantial changes in the population sizes of the principal fish species in the lake, opportunity was naturally taken to include in the programme long-term observations on the growth of the fish. These growth studies were particularly intensive in the case of the perch (*Perca fluviatilis* Linn.) as it was the species to be most reduced in numbers and was considered to be of small

average size because of the stunting effect of a very dense population. The background to the whole experiment on the fish populations of Windermere, and some of the preliminary results, have been described by Worthington (1949). The principal species of fish in Windermere are the perch, pike (*Esox lucius* Linn.), char (*Salvelinus willughbii* (Günther)), brown trout (*Salmo trutta* Linn.), eel (*Anguilla anguilla* Linn.), minnow (*Phoxinus phoxinus* Linn.) and stickleback (*Gasterosteus aculeatus* Linn.). After experiments in 1939 and 1940, the perch were trapped on a large scale each spawning season from 1941 onwards. In the winter of 1944-45 a gill-net fishery for pike was started. These two fisheries themselves provided material for investigations on the perch and pike, but at the same time some data were collected on the char and trout and other species. The fisheries for perch and pike effected considerable reductions in the densities of their populations as evidenced by the catches made by the fisheries and records from other methods of fishing. After the 1947 season large-scale trapping of perch from the north basin of Windermere was stopped and since then only samples of perch have been removed from this half of the lake.

The present paper is devoted solely to the growth of the perch in the north basin of Windermere and is based on data collected between 1942 and 1956, but which gives, with back-calculation, information on growth from 1933 onwards. It is necessary to include some data on population density but the details and methods of analysis of these data are not dealt with in the present paper. Nor are any data included on individual differences in growth or on the phenomenon, frequent in perch populations, of rare individual fish much larger than the average.

The perch in Windermere were studied by Allen (1935), who described their food and seasonal migrations. Data on the food and growth of perch in some other British waters has been published by Hartley (1947). Alm (1946) has made intensive studies of the growth of the perch and carried out several series of pond and lake experiments, with the aim of finding the causes of stunted growth. Alm also summarized the rates of growth found in Scandinavian waters by a number of other workers. Roper (1936), Kucera (1948), Krizenecky & Krizenecka-Pulankova (1951), Haakh (1929), Tesch (1955), and others have published data on the growth of perch in German and Czechoslovakian waters. There is also an extensive literature on the growth of the closely related yellow perch (*Perca flavescens* Mitchill) in North America (Carlander 1950). I published a brief preliminary paper (Le Cren 1949), which emphasized the unexpectedly slight changes in growth-rate apparent in Windermere over the period 1943-48. This conclusion is, however, considerably modified by the development in the present paper of data on growth before 1943 and since 1948.

METHODS

(*a*) *Sources and collection of material*

The traps used in the perch fishery were also used as the chief fishing method for obtaining samples. The normal fishing season lasted from the end of April until the middle of June, which is the spawning season for perch in Windermere.

In the north basin of Windermere about 300 traps were set during the period of intensive fishing and one group of about ten of these traps, set along 600 m of shore (from Wray Crag to Green Tuft), was used as the main sampling station. A large proportion, in some years all, the perch caught in this group of traps in the season were measured, sexed and aged. This series of data has been used as the main source of information on the growth-rates of the perch.

Details of the traps and their operation are given by Worthington (1949). The $\frac{1}{2}$ in. meshes will let through perch up to 9·0 cm in length and the opening will exclude the rare very big perch over about 30 cm in length. Within this range there is no evidence that the traps select perch specifically for size. In 1944 and 1945 a series of traps with $\frac{1}{4}$ in. mesh was fished alongside the standard ones. The length frequencies of the catches showed that the standard traps retained the smallest two-year-old fish although anything smaller escaped. In the spawning season the traps do select mature spawning fish and catch males more readily than females; and as is shown in a later section there are small size differences between mature and immature fish of the same age.

Other gears used for occasional or comparative sampling included seines, gill-nets and angling. The seines used were of meshes graded from 1 in. (bar) on the wings to $\frac{1}{4}$ in. (bar) in the bag. They appeared to catch a representative sample of the fish available from about 5 cm in length upwards.

Angling and gill-netting tend to be highly selective for size (Kipling 1957 and unpublished data) and material collected by these methods was avoided if possible. In order to obtain adequate data on growth before 1941 it was necessary, however, to include some angled samples, but their bias was largely avoided by excluding all the young fish whose size for age would be biased by the tendency for angling to select the larger perch available.

As well as the standard samples taken from the Green Tuft traps in the spawning season a number of other samples were analysed for age and length. A 'pilot' series of traps was set at different depths and caught small numbers of perch throughout the year. In the summers of 1944 and 1945 a number of seine hauls was made at several stations all round the north basin. In 1943 the catches from a beat of traps at Lowwood were sampled, and as occasion offered samples of perch caught at various places and times were measured and aged. All these samples showed that, while there are slight but significant differences in the growth-rate and other features of the perch from different areas in Windermere, the Green Tuft trapped samples were representative and typical of the north basin of Windermere as a whole. They also showed that, apart from the rare individual perch of exceptional size and growth, there is almost certainly no large and discrete population of perch that has been missed by both the trap fishery and the main sampling operations.

(*b*) *General methods of collecting data*

In early years the traps were lifted two or three times a week, but in later years this was reduced to weekly throughout a 6-8 week season. On each lift the

whole catch from the sample beat, or occasionally a random fraction of the catch, was sexed and measured, usually by 'pricking' the lengths on to waxed paper. In each sex-group a sub-sample, stratified to give representation to all length-groups, was measured, weighed and the operculars removed for age determination. Thus, in the early years, when catches were heavy, most of the total catch was sexed and measured, and a small stratified sample aged; from 1949 onwards the catches were nearly always small enough for all the fish to be aged. When stratified sub-sampling was carried out, the fish measured into each 0·5 cm length-group were then divided into age-groups on the basis of the smaller aged sub-sample. This resulted in the length-frequency for the whole catch being divided into a length-frequency for each age-group. From the latter were calculated the mean lengths of each age-group. In sub-sampling for age determination there was a deliberate tendency to include more of the larger fish. This gave more adequate samples of the older and rarer age-groups but it also tended to bias the representation in the younger age-groups towards too many large fish. This did not affect the means of the lengths of the age-groups as these were based on the larger random or complete samples of measured fish, but when it came to calculating the means of the back-calculated lengths some bias was apparent because fish that were larger than average when caught, tended to be larger than average in previous years of their life. In the 1943, 1944 and 1951 samples where this bias was noticeable, the frequencies of the back-calculations were weighted by the numbers of fish measured in each length-group and the bias thus eliminated. In other years the effect was considered small enough to be ignored. In most of the seined and other occasional samples all the fish were measured and aged.

Lengths were measured from the tip of the snout (with the mouth closed) to the tip of the longest normal caudal fin ray. Up till and including 1947 lengths and back-calculated lengths were measured in 0·5 cm length-groups, designated by the lower limit, but from 1948 both actual and back-calculated lengths were recorded to the millimetre below, though usually grouped later into 0·5 cm groups for the calculation of means.

The perch hatch between the middle of May and the end of June and thus by strict convention the age designation of the fish should change in the middle of the trapping season. For simplicity, however, the conventional birthday has been moved to 15 April, just before the sampling season and thus, for example, fish are called III even if they have not quite all completed three years of life.

In the collection and analysis of the data, immature and mature fish, and males and females were considered separately. Very few immature males were trapped and so they have been lumped with the mature males. Immature females have, however, been retained as a separate group.

(*c*) *Age and growth estimation*

Although length-frequency distributions have been used to help age a few samples of young fish, the vast majority of the fish were aged from the opercular bone. In most cases the opercular also provided a back-calculated estimate of

past growth. Details of the opercular method have been given in a previous paper (Le Cren 1947), but as the estimates of growth depend so much on the opercular readings a few further comments are appropriate.

Since 1947 considerably more data on the method have become available, including much more information from marked fish and further measurements of bone-length. Reading is now carried out by a slightly modified technique using better apparatus which gives considerably greater accuracy than the one previously used. The original computation of the growth ratio of the bone and fish gave a regression coefficient of 0·9202. A re-estimate of this made in 1954 based on more data gave a figure of 0·876, and this latter figure has been used in the correction of all the back-calculations in the present paper. (It might be noted here that the 1947 paper includes an error due to a mistake in transcription. Line 6 of the left-hand column of p. 197 should read: 'The standard error of $b = 0{\cdot}01104$, and $1\text{-}b = 0{\cdot}07978$, so $t = {\cdot}7226$ and thus is highly significant'.)

As experience has been gained, skill in interpreting the opercular has undoubtedly increased. About 80-90% of the Windermere opercular are easy to read and give little cause for doubt. The reading of opercular collected over a series of successive years has, however, shown that after a poor growing season the annual rings can be very close together, and only one ring may be read where two are actually present, especially at the edge of the bone. All the opercular collected in 1942 and 1943, and many of those from older fish collected in later years, were re-read in 1954 and 1955.

Many of the bones from fish angled and pilot trapped in 1942 and 1943 had suffered through being kept for several years before proper cleaning, and the slow growth made by most of the fish before 1941 and in 1942 added to the difficulties of their interpretation. Although there is little doubt about the slow general rate of growth indicated by these opercular, not quite so much confidence can be attached to the individual interpretations as in the case of bones collected since 1943, when the continuous series of annual samples has enabled a high degree of accuracy to be maintained.

(*d*) *Analysis and presentation of results*

For most of the data mean lengths were first calculated for each age-group, for each year of life, for each year of sampling. The back-calculated means were then corrected for the allometric growth of the opercular (Le Cren 1947). This correction was then applied to the corresponding Σx and Σx^2 for each group of fish (where x = individual lengths). The Σx and Σx^2 for successive sampling years were then combined to give a series for each year-class each age of its life, and the resulting combined means and standard errors calculated. For most of the data from the early year-classes (before 1939), however, and for the 1946 and 1948 year-classes for which few fish were caught, the back-calculated lengths for each fish were individually corrected for allometry and all the catches from successive years combined to give one set of mean lengths for each year-class.

Comparisons were then made between the estimates of past growth for the same

year-classes back-calculated from fish caught at different ages in different years, and '*F*' tests from an analysis of variance carried out on a series of representative year-classes. These comparisons and tests revealed that the back-calculations of length at the end of the first and second year of life showed no trend and no significant differences. The differences between several of the means for length when three, four, five and six years old were, however, rather larger, often statistically significant, and sometimes showed a trend with the means of the back-calculations from older fish being smaller. The mean-lengths for the end of the seventh or older years showed considerable variations but had no trends and the differences were not significant.

It is difficult to be certain of the case of the significant trends in back-calculated lengths that occur only in the middle-aged fish, but they are probably due to the tendency for fish that mature late to be slow growing, and to the fact that catches of fish from three to six years of age include a few individuals that are just beginning to turn into the exceptionally fast-growing fish. The absence of any significant differences between the means at the end of the first and second years of life shows that bias or errors in opercular readings are unlikely to have been the cause.

When the data were being combined into a series of mean lengths-for-age for each year-class the means derived from males caught when two years old and females caught when three years old were omitted, as were all the data for immature females. The mean lengths of these fish are presented and discussed separately.

The mean lengths for each age for each year-class represent the basic data for the various comparisons in growth-rate. Owing to chance variations (which are especially great among the rather small samples of older fish) the growth curves for length given by these data are apt to be rather irregular, and a more satisfactory picture is given by the sums of the annual increments in length. These two series of data are the same for the first three years of life in the males and four years in the females, but subsequently the mean length-for-age ($\bar{l}$) from increments have been calculated by first computing the mean length at age $x-1$ for all the fish which provide data on mean length at age x and then adding the difference between these means ($\bar{l}_x - \bar{l}_{(x-1)}$) to the mean length for all fish at age $x-1$ to obtain the mean length at age x. For example the mean length of the 168 fish of the 1940 year-class at 3 years old is 13·36 cm and for the 61 fish at 4 years old 14·60 cm, but the 61 4-year-old fish were 13·32 cm when 3 years old and thus grew 1·28 cm in their fourth year. This increment added on to the mean length of 13·36 at 3 years old gives a mean of 14·64 at 4 years old. This method of adding the increments enables use to be made of nearly all the available data without involving the irregularities caused by the loss of a large proportion of the contributing fish each successive year, and although there is some loss of accuracy through using means based on smaller numbers of fish there is an increase in the accuracy of the annual increments in length and weight which are used as the basis of most of the detailed analysis of growth. Subsequent calculations of growth in weight, etc., have been based on these sums of increments.

Weights-for-age were obtained from the empirical length-weight relationships previously established (Le Cren 1951). For each mean length a corresponding smoothed mean weight was read off an accurate log-log graph of the weight against length in September at the end of the growing season (when condition is at its maximum), the appropriate graph being used for fish of different sexes, ages and states of maturity. In the autumn of 1939 experimental traps and seines were fished and the 1322 perch caught were bulk weighed in length-groups. The mean weights for length given by these data gave relative condition factors nearly identical with similar fish caught in the autumn for 1945-48, and thus there was no change in the length-weight relationship over the first part of the experimental period. Weighings of perch from 1948-57 gave no evidence of any change in the later years, so it can be concluded that the length-weight relationship and condition of the perch have remained substantially unchanged throughout the period in spite of large changes in population density and growth-rate. Annual additive increments in weight were obtained by subtraction, and log weights and their differences (log growth-rates) calculated from the data for weight.

Thus growth data for each year-class for each sex are available in the following forms: for each age the mean length, the sum of increments in length, the mean weight (based on sum of length increments), and the log of mean weight; and for each year's growth the increment in length, the increment in weight, and the logarithmic growth-rate. Each mean length has also had its standard error and 95% confidence limits calculated for use in tests of the significance of differences. Not all these tables of data are published here, but the full tables have been deposited in the library of the Freshwater Biological Association.

In the analysis of adult growth it was discovered, as described in the next section, that the relatively constant arithmetic growth of adult perch meant that annual increment in weight was the most satisfactory measure of growth-rate, and this measure has been used most frequently in the analysis. Beverton & Holt (1958) have found that the von Bertalanffy growth formula (*e.g.* von Bertalanffy 1957) is approximated very closely by many species of fish, and is convenient to use in models of fish population dynamics. Attempts to use this formula in the present analysis were discarded after it was found that perch did not follow the von Bertalanffy form of growth at all closely.

RESULTS

(*a*) *Introduction and the basic data on growth*

Preliminary examination of the mean lengths-for-age of groups of perch showed that there were likely to be differences in growth between mature and immature fish, between males and females, and in the growth made by different year-classes. The data for these different groups were thus kept separate through the processes of collection and analysis as explained in the previous sections.

In the final analyses of the data the mean lengths of the young fish were first examined separately from the bulk of the data on mature adult fish. The mean lengths for different groups of fish at two and three years old are shown in Table 4.

Table 1. *The growth in length of perch*

The sum of annual increments in mean length (cm) for males and females of successive year-classes. Underneath each length is given in parentheses the number of fish upon which it is based. For year-classes 1933-38 inclusive all available data are combined: for year-classes after 1938 the data are from the Green Tuft traps.

	Year-classes																				
	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953
Age	MALES																				
1	6·8	6·8	7·5	6·7	7·0	6·9	6·7	6·4	5·8	5·9	6·4	6·5	6·3	5·6	7·4	5·7	8·2	6·2	6·6	6·3	6·2
	(1)	(1)	(4)	(5)	(8)	(5)	(70)	(168)	(202)	(134)	(220)	(297)	(242)	(44)	(157)	(45)	(507)	(69)	(172)	(35)	(95)
2	10·9	10·7	11·8	11·3	11·1	11·8	11·2	11·3	10·5	10·7	11·4	11·8	10·2	12·4	11·3	13·7	12·0	12·2	11·8	11·4	10·2
	(1)	(1)	(4)	(5)	(8)	(5)	(70)	(168)	(204)	(132)	(221)	(297)	(242)	(44)	(157)	(45)	(507)	(69)	(172)	(35)	(95)
3	12·4	12·2	13·4	12·5	13·1	13·6	13·4	13·4	13·2	13·6	14·0	13·4	14·0	14·4	16·4	16·2	15·3	16·1	15·7	14·0	18·8
	(1)	(1)	(4)	(5)	(8)	(5)	(70)	(168)	(203)	(132)	(221)	(297)	(242)	(18)	(157)	(33)	(507)	(69)	(172)	(35)	(95)
4	13·1	12·9	14·0	13·3	14·2	14·5	14·3	14·6	14·7	15·1	14·7	15·6	15·3	17·1	18·0	18·1	18·1	18·8	17·2	20·4	–
	(1)	(1)	(4)	(5)	(8)	(5)	(70)	(61)	(83)	(68)	(161)	(255)	(164)	(13)	(88)	(19)	(359)	(16)	(43)	(35)	
5	13·5	13·1	14·9	14·0	15·5	15·1	15·3	15·7	15·7	15·8	16·5	16·5	18·0	18·1	20·0	19·9	19·9	19·8	22·2	–	–
	(1)	(1)	(4)	(5)	(8)	(5)	(25)	(27)	(42)	(35)	(112)	(156)	(86)	(6)	(57)	(19)	(122)	(5)	(43)		
6	13·7	13·9	15·5	15·3	16·4	16·3	16·1	16·8	16·1	16·9	17·2	18·6	19·1	19·9	21·5	21·6	20·6	23·5	–	–	–
	(1)	(1)	(4)	(5)	(5)	(4)	(9)	(13)	(31)	(26)	(53)	(87)	(41)	(4)	(47)	(6)	(46)	(5)			
7	14·2	15·1	16·6	15·9	17·1	17·5	17·5	17·5	17·6	17·5	18·8	19·4	20·8	21·1	22·5	–	23·7	–	–	–	–
	(1)	(1)	(4)	(4)	(2)	(2)	(3)	(11)	(17)	(9)	(31)	(47)	(23)	(4)	(10)		(46)	–			
8	14·7	16·2	18·3	16·5	17·8	–	–	19·4	18·0	18·6	19·5	20·8	21·9	22·2	22·7		–	–	–	–	–
	(1)	(1)	(2)	(4)	(1)			(6)	(4)	(7)	(13)	(29)	(24)	(1)	(2)						
9	15·0	16·8	–	17·3	–	–	–	19·7	19·3	19·3	20·8	21·9	22·5	–	24·8	–	–	–	–	–	–
	(1)	(1)		(1)				(4)	(2)	(6)	(5)	(26)	(5)		(2)						
10	15·8	-		–	–	–	-	21·1	–	20·0	21·9	22·7	22·7	–	–	–	–	–	–	–	–
	(1)							(4)		(3)	(4)	(5)	(1)								
11	–	–	-			–	–	21·5	–	20·7	–	22·8	23·7	–	–	–	–	–	–	–	–
								(1)		(3)		(1)	(1)								
12	-	–		-	-	–	–	22·6	–	21·3	–	24·8	–	–	–	–	–	–	–	–	–
								(1)		(1)		(1)									

FEMALES

1	6·9	8·3	7·6	7·5	7·3	7·1	6·6	6·5	6·1	6·0	6·3	6·4	6·3	5·9	7·3	5·6	7·9	6·3	6·7	6·5
	(2)	(8)	(43)	(79)	(112)	(61)	(314)	(424)	(307)	(178)	(241)	(272)	(198)	(25)	(36)	(11)	(341)	(12)	(12)	(6)
2	11·9	12·3	11·7	11·6	11·4	11·1	11·2	11·5	10·7	10·8	11·1	11·5	10·1	12·6	11·2	13·3	11·7	12·4	11·7	12·4
	(2)	(8)	(43)	(79)	(112)	(61)	(314)	(425)	(307)	(177)	(241)	(272)	(199)	(25)	(36)	(11)	(341)	(12)	(12)	(6)
3	14·3	14·2	13·6	13·5	13·4	13·8	13·7	13·9	13·8	14·0	14·2	13·5	14·2	15·1	16·9	17·4	15·6	16·7	15·9	15·3
	(2)	(8)	(43)	(79)	(112)	(61)	(314)	(424)	(306)	(177)	(241)	(272)	(199)	(11)	(36)	(5)	(341)	(12)	(12)	(6)
4	15·5	14·7	14·5	14·3	14·6	15·6	14·7	15·5	15·7	15·9	15·4	16·0	15·9	18·0	19·3	19·9	18·5	19·7	17·8	22·2
	(2)	(8)	(43)	(79)	(112)	(61)	(314)	(423)	(307)	(178)	(241)	(272)	(199)	(8)	(36)	(1)	(341)	(12)	(12)	(6)
5	16·0	15·3	15·1	15·0	16·1	16·4	15·3	16·8	17·3	16·6	17·6	17·4	18·9	19·1	21·6	21·6	20·7	20·3	23·1	–
	(2)	(8)	(43)	(79)	(112)	(61)	(234)	(297)	(247)	(143)	(182)	(211)	(145)	(4)	(18)	(1)	(154)	(1)	(12)	
6	16·4	15·9	15·6	16·3	16·8	17·2	16·7	18·2	17·8	18·5	18·4	20·0	20·2	20·1	23·3	–	21·4	24·0	–	–
	(2)	(8)	(43)	(79)	(112)	(24)	(150)	(225)	(216)	(110)	(139)	(156)	(78)	(3)	(16)		(26)	(1)		
7	16·9	16·3	17·0	17·0	17·5	18·2	17·7	18·5	19·8	19·1	20·6	21·1	22·0	21·6	24·1	–	24·9	–	–	–
	(2)	(8)	(43)	(79)	(22)	(7)	(117)	(171)	(140)	(75)	(94)	(100)	(39)	(2)	(10)		(26)			
8	17·5	17·3	17·6	17·6	19·0	18·9	18·0	20·1	20·3	20·8	21·5	22·5	23·4	22·9	–	–	–	–	–	–
	(2)	(8)	(43)	(16)	(3)	(5)	(91)	(84)	(105)	(58)	(59)	(49)	(30)	(2)						
9	18·3	17·8	18·3	18·1	20·0	19·3	19·1	20·5	21·9	21·5	22·6	23·7	24·0	23·1	–	–	–	–	–	–
	(2)	(8)	(7)	(4)	(2)	(5)	(51)	(65)	(87)	(40)	(27)	(39)	(11)	(1)						
10	18·8	18·3	18·9	19·1	20·5	20·7	19·4	21·8	22·4	22·6	23·5	24·1	24·2	24·7	–	–	–	–	–	–
	(2)	(1)	(2)	(1)	(2)	(2)	(39)	(57)	(53)	(13)	(24)	(11)	(3)	(1)						
11	–	–	20·2	19·3	–	21·0	21·1	22·3	23·2	23·4	24·0	–	25·9	–	–	–	–	–	–	–
			(2)	(1)		(2)	(33)	(28)	(25)	(10)	(8)		(3)							
12	–	–	20·4	–	–	22·2	21·6	23·1	23·8	23·7	–	–	–	–	–	–	–	–	–	–
			(2)			(2)	(15)	(13)	(16)	(3)										
13	–	–	–	–	–	22·9	22·4	23·8	24·1	–	–	–	–	–	–	–	–	–	–	–
						(1)	(2)	(10)	(7)											
14	–	–	–	–	–	–	23·1	24·2	24·1	–	–	–	–	–	–	–	–	–	–	–
							(1)	(5)	(2)											
15	–	–	–	–	–	–	–	–	25·1	–	–	–	–	–	–	–	–	–	–	–
									(2)											

Table 2. *Weight (g) for age for male and female perch of successive year-classes*

Calculated from the data of Table 1 but omitting means based on less than 4 fish

Age	Year-classes																		
	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953
										MALES										
1		3·4	2·5	2·8	2·7	2·4	2·1	1·6	1·7	2·1	2·3	2·1	1·5	3·3	1·5	4·4	1·9	2·3	2·1	1·9
2		15	13	13	16	13	14	11	10	14	16	10	18	14	25	17	18	16	14	9
3		23	19	21	25	23	23	22	25	27	23	27	30	45	44	36	43	40	27	72
4		27	23	28	31	29	31	32	35	32	39	37	53	62	63	63	73	54	93	–
5		33	27	38	35	36	39	40	41	46	46	62	63	85	87	87	84	124	–	–
6		38	37	46	44	43	51	43	51	53	70	76	87	112	113	95	148	–	–	–
7		48	42	–	–	–	58	58	58	72	80	100	105	129	–	155	–	–	–	–
8		–	47				80	63	69	82	101	117	–	–	–	–	–	–	–	–
9			–				84		78	100	119	129	–	–	–	–	–	–	–	–
10		–	–				105	–		118	132	–	–		–	–	–	–	–	–
										FEMALES										
1	4·5	3·5	3·4	3·1	2·9	2·4	2·2	1·9	1·8	2·0	2·2	2·1	1·7	3·2	1·4	4·0	2·0	2·4	2·3	
2	19	16	15	15	13	14	15	12	12	13	15	10	21	14	25	16	20	16	19	
3	28	25	24	23	26	25	26	25	27	28	24	28	35	51	56	39	49	41	36	
4	32	30	29	31	39	32	38	40	42	36	43	41	63	80	–	70	84	61	126	
5	36	35	34	43	46	37	49	55	45	59	56	74	78	114	–	99	–	145	–	
6	41	38	45	50	54	49	66	61	70	68	89	92	–	148	–	112	–	–	–	
7	45	52	52	57	66	60	69	86	76	97	106	122	–	166	–	185	–	–	–	
8	55	58	58		75	63	91	94	102	113	133	151	–		–			–	–	
9	61	66	64	–	80	77	96	121	113	133	158	165	–	–	–	–		–	–	
10	–	–	–	–	–	81	120	129	133	152	165	–	–	–	–	–	–	–	–	
11	–	–	–	–	–	106	127	146	152	165	–	–	–	–	–	–	–	–	–	
12	–	–	–	–	–	115	145	160												
13		–	–	–	–	–	160	165	–	–	–	–	–	–	–	–	–	–	–	
14							166													

Table 3. *Annual increments in weight (g) for male and female perch of successive year-classes*

Calculated from the data of Table 2

Year of growth	Year-classes 1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953
									MALES											
1		3·4	2·5	2·8	2·7	2·4	2·1	1·6	1·7	2·1	2·3	2·0	1·5	3·3	1·5	4·4	1·9	2·3	2·1	1·9
2		12	11	10	13	10	11	9	8	12	13	8	17	10	24	12	16	14	12	7
3		8	6	9	9	10	9	11	15	13	7	17	12	31	19	19	25	24	13	63
4		4	4	7	6	6	8	10	10	5	16	10	23	17	19	27	30	14	66	–
5		6	4	10	4	7	8	8	6	14	7	25	10	23	24	24	11	70	–	–
6		5	10	8	9	7	12	3	10	7	24	14	24	27	26	8	64	–	–	–
7		10	5	–	–	–	7	15	7	19	10	24	18	17	–	60	–	–	–	–
8		–	5	–	–	–	22	5	11	10	21	17	–	–	–	–	–	–	–	–
9		–	–	–	–	–	4	–	9	18	18	12	–	–	–	–	–	–	–	–
10		–	–	–	–	–	21	–	–	18	13	–	–	–	–	–	–	–	–	–
									FEMALES											
1	4·5	3·5	3·4	3·1	2·9	2·4	2·2	1·9	1·8	2·0	2·2	2·1	1·7	3·2	1·4	4·0	2·0	2·4	2·3	
2	14	11	12	11	10	10	13	10	10	11	13	8	19	11	24	12	18	14	17	
3	9	9	9	9	13	12	11	13	15	15	9	18	14	37	31	23	29	25	17	
4	4	6	5	8	13	6	12	15	15	8	19	13	27	29	–	31	35	20	90	
5	5	4	5	12	8	5	11	15	3	23	13	33	15	34	–	29	–	84	–	
6	5	4	11	7	8	12	17	6	25	9	33	18	–	34	–	13	–	–	–	
7	5	13	7	7	11	11	3	25	6	29	17	30	–	18	–	73	–	–	–	
8	9	7	6	6	9	3	22	8	26	16	27	29	–	–	–	–	–	–	–	
9	6	8	–	–	5	14	5	27	11	20	25	14	–	–	–	–	–	–	–	
10	–	–	–	–	–	4	24	7	20	19	7	–	–	–	–	–	–	–	–	
11	–	–	–	–	–	26	7	17	19	13	–	–	–	–	–	–	–	–	–	
12	–	–	–	–	–	8	18	14	–	–	–	–	–	–	–	–	–	–	–	
13	–	–	–	–	–	–	15	5	–	–	–	–	–	–	–	–	–	–	–	
14	–	–	–	–	–	–	6	–	–	–	–	–	–	–	–	–	–	–	–	

The remaining basic data from mature fish from the Green Tuft traps (supplemented for the 1933-38 year classes by data from additional sources) are shown in Tables 1 to 3. These tables give for males and females, the mean lengths at each age of each year-class and the corresponding calculated weights for age and increments in weight for each year of life.

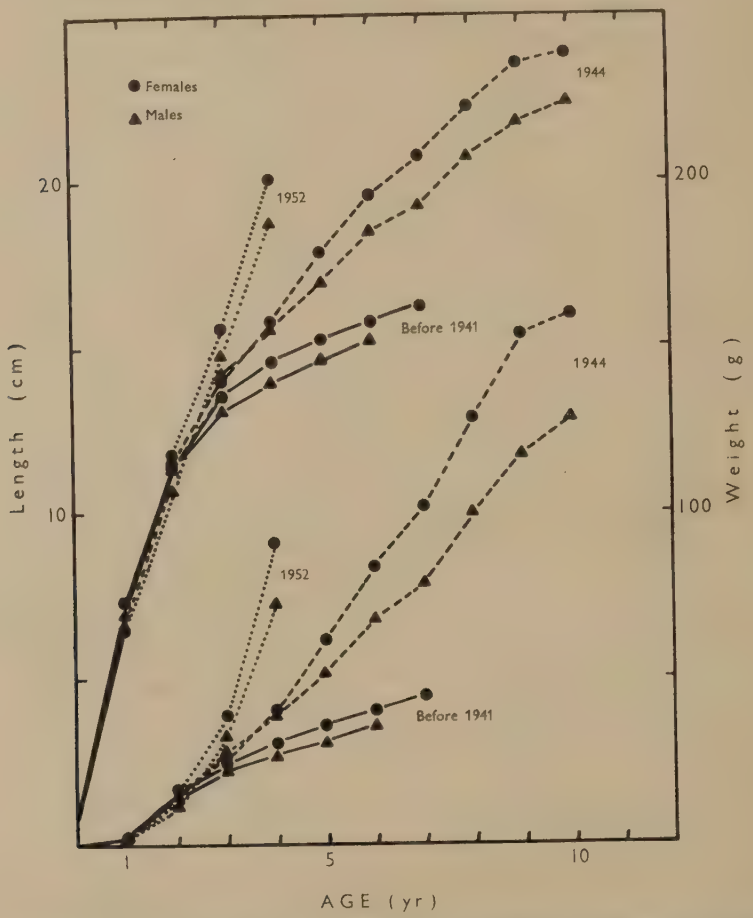

Fig. 1. Length-for-age and weight-for-age growth-curves for male and female fish of the combined year-classes before 1941, and the 1944, and 1952 year-classes. The data have been adjusted for year-to-year temperature variations.

The analyses of all these data revealed seven main features of interest:

(1) Growth in the first two years was similar for males and females but fish mature or about to mature at two or three years old were larger on average than immature or late maturing fish of the same age.

(2) Adult females tended to grow faster than adult males (Fig. 1).
(3) There were year-to-year fluctuations in growth which appeared to be correlated with calendar year.
(4) Apart from year-to-year fluctuations, once adult fish of each year-class tended to have a constant annual increment in weight regardless of age (Figs. 1 and 2).
(5) Over the period of observation there appeared to be no trend in the growth-rate in the first two years of life (Fig. 8).
(6) The growth-rate of the adult fish, however, increased in 1941 and maintained a higher rate since then (Fig. 10).

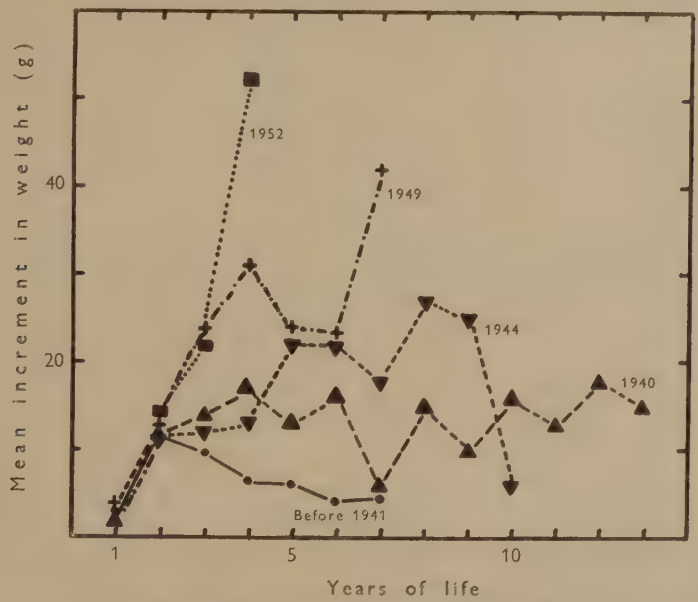

Fig. 2. Annual increments in weight plotted against age for female fish of the combined year-classes before 1941 and the 1940, 1944, 1949 and 1952 year-classes.

(7) Since 1941 each successive year-class tended to grow faster and have a greater average annual increment in weight (Fig. 11).

Each of these features will now be discussed in turn in greater detail in the subsequent sections.

(*b*) *Differences in growth between the sexes and mature and immature fish in the first three years of life*

The data for the back-calculated mean lengths at the end of the first year of life (Table 1) show no consistent difference between males and females, though there is some variation between the year-classes. An analysis of variance was made of these data using a test based on the means weighted with the reciprocals of the numbers of fish from which they were derived (Snedecor 1946, p. 289). The means of the weighted mean lengths were 6·46 for males and 6·50 for females; the

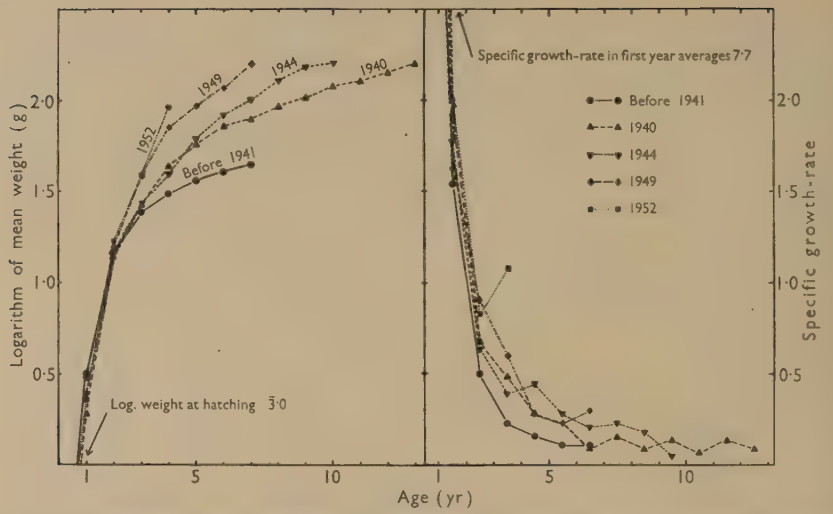

Fig. 3. The logarithm of weight against age (left) and specific growth-rate against age (right) for female fish of the combined year-classes before 1941, and the 1940, 1944, 1949 and 1952 year-classes. (The specific growth rate is calculated from $\log_e W_{(x+1)} - \log_e W_x$ where W = mean weight and x = age in years).

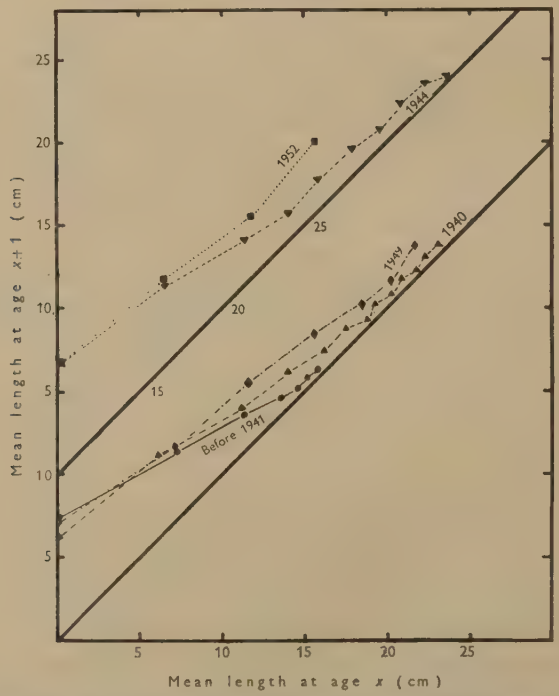

Fig. 4. Ford-Walford plots of the mean length at age $(x+1)$ against the mean length at age x for female fish of the combined year-classes before 1941, and the 1940, 1944, 1949 and 1952 year-classes.

slight difference between them is not significant. There is, however, a highly significant difference between the mean lengths of the different year-classes when one year old.

As very few immature two-year-old males were caught, they were lumped in the analysis with the mature two-year-old males. All the females caught when two years old were immature, however, and separate mean lengths were calculated for them. Not all the females matured in their third year and so two series of mean lengths were calculated from three-year old females, one from mature fish and the other from immatures. Nearly all the females caught when four or more years old were mature; the small numbers of old immatures did not warrant a detailed examination of their back-calculated lengths. There were thus available, from actual and back-calculated measurements, six series of mean lengths at two years of age: (1) males caught when two years old, (2) males caught when three or older, (3) females caught when two (all immature), (4) immature females caught when three, (5) mature females caught when three, and (6) mature females caught when

Table 4. *Weighted mean lengths of different sex groups when two and three years old*

Group	Sex	Age and maturity when caught	Mean length when II (cm)	Mean length when III (cm)
1	Male	II nearly all mature	11·61	–
2	,,	III and older, nearly all mature	11·28	14·49
3	Female	II Immature	11·61	–
4	,,	III Immature	10·92	14·46
5	,,	III Mature	11·26	15·10
6	,,	IV and older, mature	11·19	14·84

four or older. In addition there were four series of mean lengths at the age of three years (groups 2, 4, 5 and 6). The mean lengths for each sex-maturity group for the 1941-50 year-classes (but omitting the 1946 and 1948 year-classes because of inadequate data) were treated with reciprocal weighting in a similar way to those for the first year's growth and the resultant means are shown in Table 4. Analysis of variance tests showed that the differences between the sex groups and year-classes were highly significant for the lengths at both two and three years of age.

It will be seen that the mean lengths for male and female fish caught when two years old (groups 1 and 3) are identical and greater than the other means back-calculated from fish caught when older. This difference is highly significant statistically, but is probably an artificial effect due to some selection of larger two-year-olds by the traps.

Individual tests of significance showed that when they were two years old there was no significant difference between the mature males and females back-calculated from older fish (groups 2 and 6) but when they were three, the larger size of the females is highly significant. Within the females the three-year-old immatures (group 4) were significantly smaller than the mature females (groups 5 and 6) both when two and three years old. Within the mature females, those caught when three years old (group 5) were larger than those caught when older (group 6) both at two and three years of age, but at two the difference is not significant.

The age and size of perch at maturity has been reviewed by Alm (1946). He found little consistent difference between the sizes of young male and female perch and the similar growth shown by the sexes for the first two years of life is probably typical of perch in general. Maturation appears to be correlated with both size and age but the analysis of the relative importance of the two factors is complicated because while size and growth-rate can vary continuously, the age of first spawning can vary only in units of whole years. In Windermere there is evidently a tendency for the larger individuals to mature earlier (or early maturing fish to grow faster) and this was even more apparent in Alm's experiments. Both in Windermere and in Alm's tarns and ponds, however, there was considerable individual variation so that immature fish larger than mature individuals of the same age were quite frequent. The slower growth of the mature males compared to the maturing females in the third year cannot be solely due to the males having spawned at the beginning of their third year as immature females grew no faster than the males. It can be concluded that there are real and consistent but small differences in growth correlated with age of maturity, and after maturation with sex, but the causal relationships of these differences are still obscure.

(*c*) *The differences between the sexes in adult growth*

Examination of Table 2 reveals that in nearly every case the mean length at the end of the third and subsequent years is greater for females than males of the same age and year-class. This difference is also shown in Tables 3 and 7 where the annual increments in weight are given, and in Fig. 1 which shows for comparison the growth of males and females before 1941 and of the 1944 and 1952 year-classes. Examination of the data on growth before and after the start of the population changes in 1941 shows that the sex difference in growth was present both before and after 1941, and was relatively unaffected by the great changes in growth-rate that started in 1941. Table 10 summarizes the data on growth before 1941 and it will be seen that from the third year onwards the females grew faster than the males, though the few males available grew slightly faster in the sixth year. On average the annual weight increments of the females was about 120% of that of the males. (The annual weight increments for adults given in Tables 11 and 12 are not valid for comparisons between the sexes, as the fast third-year growth is included in the averages for males but not in those for females.)

The females of the 1935-40 year-classes continued to grow faster than the males after 1941 (Table 12) and averaged about 113% of the annual weight increment of the males. In the year-classes hatching from 1941 onwards the difference in growth-rate was rather larger, the females adding about 130% of the male annual weight increment and in the most recent year-classes the difference has tended to be even greater (Table 12). The change in this sex-differential in growth has not, however, been large over the period and there is no significant difference in the rates of increase in growth-rate in the two sexes (§ *g*). A real and consistently faster growth-rate for adult females seems to be a feature of the perch in Winder-

mere as has been found in a number of other waters (Alm 1946, Hartley 1947, Kucera 1948, Le Cren unpublished data). This difference appears to be very slight in some slow growing populations (Alm 1946, Tesch 1955) and not apparent in a few cases (Krizenecky & Krizeneka-Pulankova 1951).

(d) Fluctuations in growth with calendar year and their correlation with temperature

Superficial examination of the operculars without any calculation of actual growth showed quite clearly that the growth of the perch in 1946 and 1948 was much less than usual, while in 1947 and 1949 it was exceptionally good. As the summers of 1946 and 1948 were rather cool and sunless but those of 1947 and 1949 exceptionally hot, sunny and long, it was decided to compare the annual fluctuations in growth with the annual fluctuations in some measure of temperature.

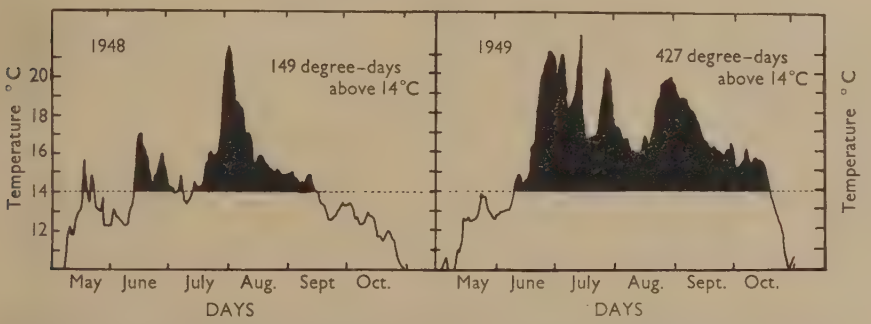

Fig. 5. Surface water temperature graphs for the summer months in Windermere in 1948 (an unusually cool summer) and 1949 (an unusually hot summer). The black areas were measured to give the degree-days over 14° C.

Surface water temperatures have been taken at 0900 h on each weekday since 1933 at the shore of Windermere near to the Freshwater Biological Association's laboratory; at Wray Castle (which is very near Green Tuft) until September 1951 and at The Ferry House since then. These temperatures have been used for these correlations with growth. Since 1947 weekly temperature data for the surface (at approximately 1100 h) above the deepest point of Windermere in the middle of the North Basin are available. These data give rather higher temperatures in hot weather but similar though slightly lower temperatures for colder weather. Both these sets of data should give a fairly good indication of the temperature of the littoral epiliminion water inhabited by the perch in summer. The temperatures taken at Wray Castle Boathouse and the Ferry House were used for nearly all the correlations. The temperature data from the middle of the lake were, however, used for one pair of comparative correlations and they gave a slightly higher correlation coefficient than the other temperature data (Table 6); this may be due to their greater range of variation.

It is known that most of the growth of the perch in Windermere takes place in the period from June to September. Examination of graphs of surface water

temperature plotted against days showed that this period roughly coincided with the period when the temperature was above 14° C (Fig. 5). As a first test a correlation coefficient was calculated for adult growth and the number of days that the water temperature was above 14° C. This gave a value for r of 0·72 which was highly significant for the 15 pairs of observations on which it was based. Next, however, the areas of the temperature graphs were measured with a planimeter giving a measure of degree-days over 14° C (Fig. 5). A preliminary calculation of a correlation coefficient for degree days and adult growth gave $r = 0·78$

Table 5. *Year-to-year fluctuations in temperature and growth*

The right-hand column gives the number of age-groups contributing to each mean of % average growth for male + female adult fish.

	Temperature (degree-days above 14° C)	Weight Increments: 1st year (g)	2nd year (g)	3rd year female (% running average)	Adult male (% average)	Adult female (% average)	Adult male + female (% average)	Number of age-groups adult male+female
1934	294	4·5	–	–	–	–	–	–
1935	306	3·5	14·3	–	–	–	–	–
1936	253	3·4	11·4	95	–	–	–	–
1937	300	3·1	12·1	91	140	84	112	2
1938	190	2·9	11·3	88	101	111	106	4
1939	345	2·4	10·4	88	102	97	100	6
1940	325	2·2	10·3	120	88	99	94	6
1941	305	1·7	12·3	103	125	136	132	8
1942	165	1·7	9·5	85	66	80	76	10
1943	180	2·1	9·3	101	98	79	88	11
1944	231	2·2	11·6	120	105	104	104	9
1945	295	2·1	13·0	104	98	110	103	9
1946	126	1·6	7·5	64	47	36	41	11
1947	426	3·2	18·0	98	125	147	136	12
1948	149	1·5	10·5	64	55	49	52	14
1949	427	4·2	23·6	149	159	177	169	15
1950	255	2·0	12·2	116	77	80	79	16
1951	280	2·4	16·7	79	117	127	122	14
1952	279	2·2	13·6	117	109	113	111	16
1953	345	1·9	14·5	75	87	57	72	14
1954	145	–	7·3	44	35	38	36	6
1955	503	–	–	–	198	180	192	6

(Table 6). On the basis of this result the degree-days over 14° C were estimated from the areas of graphs of temperatures for all the years from 1934 to 1956 and used in the subsequent calculations.

The results of these measurements of temperature and the data that are available for growth at different ages are tabulated in Table 5. In the case of the growth in the first and second years the mean increments for male and female fish were averaged as it had been shown that there was no significant difference between them. The growth for these years could be expressed simply as weight increment as there was no trend throughout the period. Weight increment was chosen as giving the best measure of growth, after increment in the logarithm of weight

(specific growth-rate) had been found to give a much poorer correlation with temperature. For the adult fish, however, as there were marked long-term increases in growth-rate over the period, it was necessary first to obtain a basis with which the year-by-year fluctuations might be compared, and the different growth-rates of the two sexes and successive year-classes allowed for. As it appeared from the data of Table 3 that after becoming adult, fish in any one year-class had a fairly constant annual increment in weight regardless of age, a mean annual increment in weight was calculated for each year-class for each sex and the actual increment made in each year then expressed as a percentage of this mean. When these percentages were tabulated according to calendar years, it was clear that both sexes and all the year-classes showed similar fluctuations with calendar year,

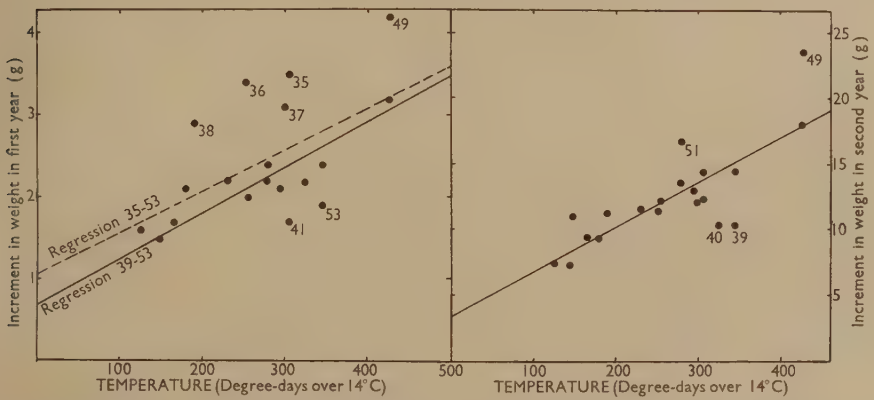

Fig. 6. Left, weight increment for the first year plotted against summer surface water temperature (degree-days over 14° C). The upper line is the least-squares regression for all the year-classes, the lower line the regression for all the year-classes since 1939. Right, weight increment for the second year plotted against temperature. The line is the least-squares regression for all the year-classes.

and mean percentages were then calculated for each year. These mean percentages for males, females and both sexes combined are shown in Table 5 together with the number of individual percentages from different age-groups (or year-classes) which contributed to the mean for both sexes.

Examination of the data for the growth of female fish in their third year revealed that the growth of successive year-classes showed some trend over the period, but did not increase as fast as the growth of the adults. Eventually it was decided to use a moving average based on the average third-year growth over a period of five years for comparison with the actual increment made in the middle year of the five-year period.

Examination of Table 5 and Figs. 6 and 7 which are based on it, shows that all ages show consistent variations in growth and that these appear to be related to the temperature during the growing period in each year. This relationship was further investigated by the calculation of a series of correlation coefficients. The details of these correlations are set out in Table 6. All the correlation-coefficients

Table 6. *Correlations between growth and temperature, and data for regressions and covariance of growth on temperature*

The two lower pairs of correlations are included to give comparisons between temperatures measured at the buoy at the centre of the lake* and at the shore as in the other correlations, and between temperature expressed as the number of days when it was above 14° C† and degree days above 14° C as in the other correlations.

Group of fish	Range of years	r	Number of observations	Regression coefficients			Sums of squares for growth			Regression as % total	F
				a	b	b when growth %	Regression	Residual	Total		
1st year	1935-53	0·58	19	1·05	0·0051	0·209	3·40	6·54	9·94	34	8·83
1st year	1939-53	0·76	15	0·68	0·0056	0·251	3·80	2·77	6·57	58	17·8
2nd year	1935-54	0·79	20	3·43	0·0340	0·272	168	100	268	63	30·2
3rd year	1936-54	0·59	19	52·52	0·1600	0·160	3691	6982	10 673	34	8·98
Adults	1937-55	0·71	189	11·84	0·3179	0·318	191 318	188 573	379 895	50	188
2nd year	1947-54	0·90	8	not calculated							
*2nd year	1947-54	0·93	8								
†Adult means	1939-53	0·72	15								
Adult means	1939-53	0·78	15								

(r) are statistically highly significant, but those for the first-year growth from 1935-53 and for the third-year growth of females are only just so. As well as correlation coefficients, regressions of growth on temperature were calculated by the usual method of least squares, using the same basic data, and details of these as well are given in Table 6. The F tests on these regressions give the same results of significance as the values of r.

The two correlations and regressions calculated for first-year growth and Fig. 6 show that the growth for the years 1935-38 inclusive is much greater than would be expected. Although there is no obvious explanation of this, these data were back-calculated from rather old fish caught in 1942 and 1943 and may be biased. The second set of calculations omitting the data before 1939 gives results similar to those obtained for second-year and later growth. Although 1949 was an exceptionally warm and long summer the fry of that year evidently grew even more than would be expected, as the point for 1949 lies considerably above the regression line. There is no obvious explanation either why growth in 1941 and 1953 should be considerably less than that expected.

Growth in the second year shows very good correlation with temperature and most of the points lie close to the regression line (Fig. 6); growth in 1949 was, however, again above that expected. The points for the growth of females in their third year show considerably more scatter and the correlation is not so good. This may be due partly to the lack of a suitable basis for eliminating the effect of the general increase in third-year growth through the period of observation. For example 1954 was a poor year for growth with a low temperature, but it becomes exceptionally poor when compared to the average for the five-year period 1952-56 as this included some unusually good years.

The correlation and regression for adult growth were calculated from the individual percentage increments of the separate year-classes present as adults each year, and not the means of these percentages given in Table 5. There is thus a considerable scatter of points in Fig. 7. The correlation coefficient is nevertheless quite high, and the regression line appears to provide a good average measure of the effect of temperature on growth. It will be seen that the mean percentages for each year do show some variation from the line. The points for 1953 and 1954 are well below the line, while those for 1938, 1941, 1949 and 1955 are unexpectedly high.

The values for the regression coefficients b given in Table 6, and especially those adjusted to a comparable percentage-growth basis, show that temperature has the greatest effect upon the growth of the adults but rather less effect on second- or first-year growth, though the differences between the regression coefficients are not statistically significant. The analysis of the sums of squares for growth given in Table 6 shows that for the first-year, second-year and adult growth the regression on temperature accounts for half or more of the year-to-year variation; for the second-year growth nearly two-thirds of this variation could be associated with temperature. For the adults it was possible to carry the analysis of the sums of squares further and distinguish that due to the variation in mean growth from

year to year and that due to variation from the means of the individual year-classes or age-groups of fish of each sex. This analysis showed that of the 50% of the sums of squares remaining after the regression, 23% were due to the significant variation of the means from the regression, in other words year-to-year variation in growth not attributable to temperature, and the remaining 27% due to variation of the growth of individual age-groups within any one year. Temperature thus

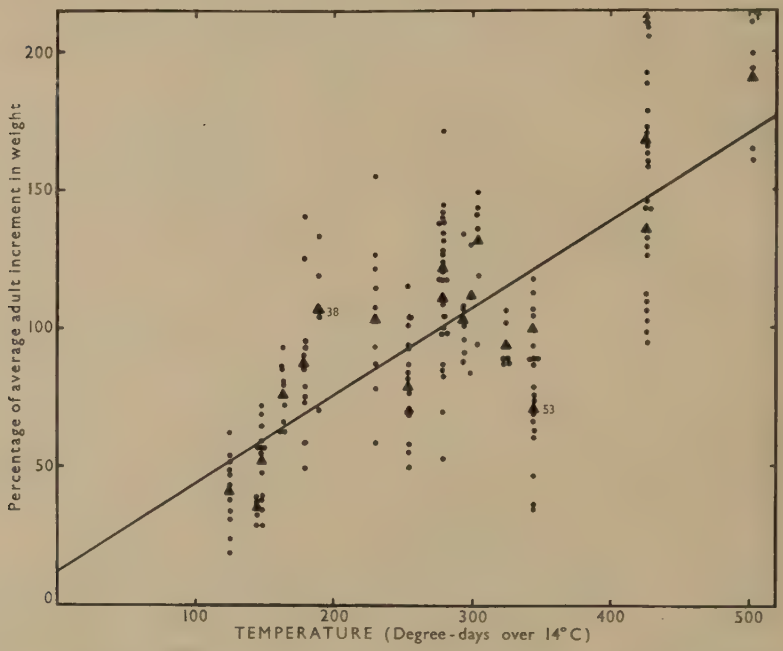

Fig. 7. Adult growth and temperature. Percentage of average annual increment when adult for each year-class for each year plotted against summer surface water temperature. The small points are for individual year-classes of each sex, the larger triangles are the means for each year of all year-classes and both sexes. The line is the least-squares regression for all the small points.

accounts for about two-thirds of that year-to-year variation in growth not attributable to chance or differences between age-groups.

It is noticeable that the variations in growth due to temperature are quite large. A frequency analysis of the temperature data over a period of twenty-four years shows that on expectation the adult growth will be as low as 35% or as great as 165% of the normal average about once every twenty years, and one year out of every three the growth will differ from the average by about 32%.

The values of the regression coefficient *a* shown in Table 6 suggest that 14° C was about the right temperature to take as a base line from which to measure the degree-days. In all the regressions *a* is positive, however, which does suggest that growth might be more directly proportional to the temperature above a slightly

lower value, perhaps about 13·5° C. These data do therefore corroborate other observations that suggest that growth begins in the spring when the water temperature reaches about 13-14° C.

The rather scanty and not quite comparable data on growth before 1941 have been included in the above analysis as far as possible. There is a noticeable tendency for the correlation between growth and temperature to have become more marked since 1941, particularly in the later years. This could be due to the reduction in population density releasing the growth-rate from a restraining influence and thus rendering it more liable to the effects of other environmental factors. On the other hand the apparently less pronounced correlation between growth and temperature in the earlier years may be due to the less reliable data that are available for those years. The period from 1946 to 1955 also included a number of years with exceptionally low or high temperature, a degree of variation that was absent from the earlier period from 1934 to 1945.

It is pertinent to consider briefly the ways in which the water temperature could affect the growth of the perch. The effect of temperature on the growth of fish has long been known as important, and several species of non-salmonid fish are known to grow only in the summer months. Temperature could affect the growth-rate either directly or by increasing the food supply. As the perch feeds on a variety of food animals from small zooplankton to small fish, and changes the broad features of its diet from plankton to benthos at a length of about 13 cm (or an age of 2+ years), and from benthos to fish at about 18 cm (Allen 1935), it is unlikely that temperature will affect all these prey animals similarly, and that there will be immediate increases in their abundance with increases in temperature. It is probable therefore that most of the effect of temperature is a direct one on the physiology of the fish.

It is also interesting to note that as well as marked year-to-year variations in growth-rate there are considerable variations in brood success, probably due mainly to differences in the rates of survival of the fry in different years (Le Cren 1955). These variations are also climatically induced, and although they do not appear to be correlated so closely to temperature as is growth, it is notable that the 1946, 1948 and 1950 year-classes were very weak, while that of 1949 was exceptionally strong; 1949 has already been noted as a year of exceptional fry growth. Data on the strength of a sufficient number of year-classes are not yet available for a more detailed comparison.

Having established a relationship between growth and summer water temperature it was possible to use the calculated regressions to adjust the data on growth for the year-to-year variations in temperature and thus eliminate much of the fluctuations shown by these data. For the first and second year data the increments observed for each year were adjusted to the mean temperature for all the years on which the regressions were based. For the third-year females and adults smoothed mean values of percentage growth expected each year were calculated from the regression formulae and the observed temperatures for each year. The individual growth increments were then proportionally adjusted by the ratio of

Table 7. *Annual increments in weight (g) adjusted for annual temperature differences for male and female perch of successive year-classes*

Year of growth	Year-classes																			
	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953
									MALES											
1		3·3	2·6	2·7	3·2	2·0	1·9	1·5	2·3	2·7	2·5	2·0	2·3	2·4	2·1	3·6	2·1	2·3	2·1	1·5
2		12·4	9·8	13·7	10·2	8·4	10·2	12·3	11·3	13·0	12·3	12·3	11·6	14·3	18·2	12·6	15·2	13·1	9·1	11·4
3		7·8	7·2	7·4	7·9	9·7	14	16	18	12	13	12	21	20	20	19	25	20	22	37
4		4·7	3·8	6·0	5·6	9·4	12	12	9·5	10	11	17	16	18	19	27	25	24	39	–
5		5·4	3·3	8·6	6·7	10	9·4	7·6	12	10	13	17	11	23	24	20	19	41	–	–
6		3·7	8·6	13	14	7·9	11	5·8	6·8	12	16	15	24	27	21	14	38	–	–	–
7		9·2	7·8	–	–	–	13	10	12	13	11	24	18	14	–	35	–	–	–	–
8		–	8·6	–	–	–	15	8·5	7·5	11	21	17	–	–	–	–	–	–	–	–
9		–	–	–	–	–	6·8	–	10	18	18	10	–	–	–	–	–	–	–	–
10		–	–	–	–	–	14	–	–	18	11	–	–	–	–	–	–	–	–	–
									FEMALES											
1	4·3	3·4	3·5	3·0	3·4	2·0	1·9	1·7	2·4	2·6	2·5	2·0	2·5	2·4	2·1	3·1	2·1	2·4	2·3	
2	12·9	11·7	10·8	15·3	7·6	8·3	11·8	13·5	13·1	12·6	11·7	12·3	13·6	14·8	18·1	12·6	17·2	13·4	14·5	
3	9·8	9·0	10	8·3	12	11	14	16	17	15	12	15	19	31	34	24	30	23	22	
4	3·4	7·8	3·9	6·8	11	9·8	17	18	14	15	13	22	19	31	–	31	29	35	52	
5	6·4	3·5	4·7	11	12	7·2	13	14	12	16	22	22	16	34	–	24	–	49	–	
6	3·9	3·7	9·8	11	12	14	16	12	17	15	22	19	–	34	–	23	–	–	–	
7	3·9	12	11	9·9	13	10	5·8	17	10	20	18	30	–	15	–	42	–	–	–	
8	8·5	10	8·3	–	8·1	6·0	15	15	18	17	27	29	–	–	–	–	–	–	–	
9	9·7	11	7·0	–	9·5	9·7	10	18	12	20	25	11	–	–	–	–	–	–	–	
10	–	–	–	–	–	5·9	16	7·5	20	19	5·8	–	–	–	–	–	–	–	–	
11	–	–	–	–	–	18	7·5	17	19	11	–	–	–	–	–	–	–	–	–	
12	–	–	–	–	–	9·0	18	14	–	–	–	–	–	–	–	–	–	–	–	
13	–	–	–	–	–	–	15	4·1	–	–	–	–	–	–	–	–	–	–	–	
14	–	–	–	–	–	–	4·9	–	–	–	–	–	–	–	–	–		–		

Table 8. *Weight (g) for age adjusted for annual temperature differences for male and female perch of successive year-classes*

Calculated from the data of Table 7

	Year-classes																			
	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953
Age									MALES											
1		3·3	2·6	2·7	3·2	2·0	1·9	1·5	2·3	2·7	2·5	2·0	2·3	2·4	2·1	3·6	2·1	2·3	2·1	1·5
2		15·7	12·4	16·4	13·4	10·4	12·1	13·8	13·6	15·7	14·8	14·3	13·9	16·7	20·3	16·2	17·3	15·4	11·2	12·9
3		23	20	24	21	20	26	30	32	28	28	26	35	37	40	35	42	35	33	50
4		28	23	30	27	30	38	42	41	38	39	43	51	55	59	62	67	59	72	–
5		34	27	38	34	40	47	50	53	48	52	60	62	78	83	82	86	100	–	–
6		37	35	51	47	48	58	56	60	60	68	75	86	105	104	96	124	–	–	–
7		46	43	–	–	–	71	66	72	73	79	99	104	119	–	131	–	–	–	–
8		–	52	–	–	–	86	74	79	84	100	116	–	–	–	–	–	–	–	–
9		–	–	–	–	–	93	–	89	102	118	126	–	–	–	–	–	–	–	–
10		–	–	–	–	–	107	–	–	120	129	–	–	–	–	–	–	–	–	–
									FEMALES											
1	4·3	3·4	3·5	3·0	3·4	2·0	1·9	1·7	2·4	2·6	2·4	2·0	2·5	2·4	2·1	3·1	2·1	2·4	2·3	
2	17·2	15·1	14·3	18·3	11·0	10·3	13·7	15·2	15·5	15·2	14·1	14·3	16·1	17·2	20·2	15·7	19·3	15·8	16·8	
3	27	24	25	27	23	22	27	31	32	30	27	29	35	48	54	39	49	39	39	
4	30	32	29	33	34	32	44	49	46	45	40	51	54	79	–	70	79	74	91	
5	37	35	33	44	46	39	57	63	58	61	62	73	70	113	–	94	–	123	–	
6	41	39	43	56	58	53	73	75	73	76	84	91	–	147	–	117	–	–	–	
7	45	51	54	66	71	63	79	92	83	96	102	121	–	162	–	159	–	–	–	
8	53	61	63	–	79	69	94	107	101	113	129	150	–	–	–	–	–	–	–	
9	63	73	70	–	89	79	104	125	113	133	154	161	–	–	–	–	–	–	–	
10	–	–	–	–	–	85	120	133	133	152	160	–	–	–	–	–	–	–	–	
11	–	–	–	–	–	103	128	150	152	163	–	–	–	–	–	–	–	–	–	
12	–	–	–	–	–	112	146	164	–	–	–	–	–	–	–	–	–	–	–	
13	–	–	–	–	–	–	161	168	–	–	–	–	–	–	–	–	–	–	–	
14	–	–	–	–	–	–	166	–	–	–	–	–	–	–	–	–	–	–	–	

smoothed mean percentage to 100%, thus bringing the growth increment to what it would have been expected to have been in a year of average temperature. As there is evidence that the variance in growth increases with the temperature and the relationship is a proportional one, this proportional correction seemed to be more valid than the usual method of an additive adjustment to the dependant variate. These adjusted data of weight increments and weight for age are shown in Tables 7 and 8, and are used in much of the following consideration of aspects of growth other than the effects of year-to-year variations in temperature.

(e) Trends in growth in the first and second years of life

The data for the growth made by 0-group and I-group perch for males and females combined are shown in Table 12. These data have been adjusted for temperature and are shown plotted in Fig. 8. It will be seen from this figure that

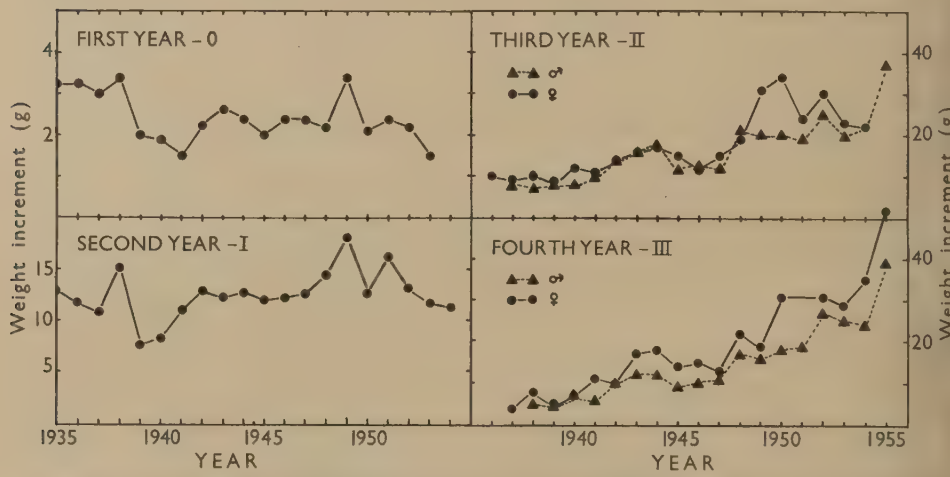

Fig. 8. The increments in weight, adjusted for temperature variations, made by perch in their first, second, third and fourth years, for each year from 1935 to 1955.

apart from the high values for the first four years, 1935 to 1938, and an unusually high value for 1949, the weight of the perch at the end of the first year is very similar throughout the period. The cause of the high values obtained for 1935-38 is not known but they may be due to bias in the back-calculation of the growth from the small number of old and difficult operculars in poor condition on which the data are based. No direct estimates are possible of the changes in the population density of 0-group perch that occurred over the period of observation, but it is possible to estimate both the relative density of egg deposition from which the fry hatched, and also the density of adult survivors of the same year-classes (Table 12). Egg numbers showed variations of more than six-fold and adults changes of up to one-hundredfold in the period but no correlation is shown

between growth and either measure of relative density. The data for weight-increment in the second year show a little more variation, but again there is no general trend. There is no obvious explanation for the poor growth of the yearlings in 1939 and 1940, and 1949 seems to have been an exceptional year for growth for fish of all ages, even when allowance is made for its warmth. The catches of the adults of each year-class when III and IV give a good indication of their relative abundance and thus the relative strengths of the year-classes and density of yearling fish. When the growth made in the second year is plotted against density a tendency is apparent for the weakest year-classes to grow faster (Fig. 9), and in order to investigate this further partial correlation coefficients were calculated for the four variables growth (as expressed by increment in log weight), year-class

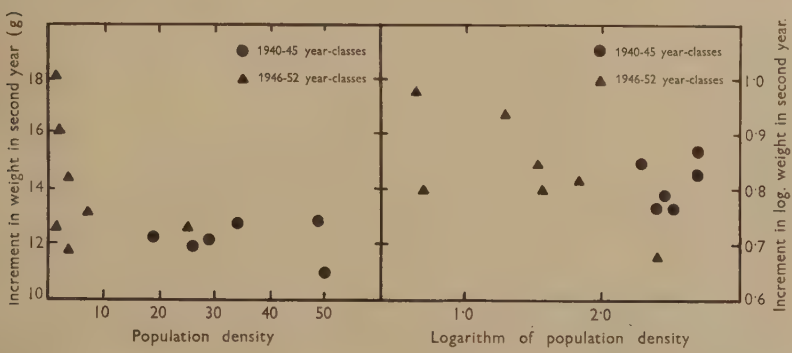

Fig. 9. Second-year growth and population density. Increment in weight in the second year (I-group fish) plotted against an estimate of relative abundance of the same fish (I-group). The population density is estimated from the catches of adult fish in traps two and three years later. The left-hand graph is arithmetic but in the right-hand graph both scales are logarithmic.

strength, total abundance of adult fish, and year, for the thirteen successive year-classes 1940-52. The correlation coefficients showed that when the effects of the other variables, abundance of adults and year, were eliminated there was a highly significantly negative correlation between growth and abundance for fish in their second year ($r = -0{\cdot}768$ for 9 degrees of freedom). The partial correlation for growth and the abundance of adult fish was positive and just significant ($r = +0{\cdot}603$); there is no obvious explanation for this. There was no significant correlation between growth and year. Figure 9 indicates that the negative correlation between growth and population density in the second year is largely due to the greater growth made by very weak year-classes, and it is clear that there has been a greater degree of correlation among the more recent year-classes.

The average increments in weight for the young perch in Windermere are 2·22 g for the first year and 12·52 g for the second year. This means that the average perch has grown to a weight of 14·7 g and a length of 11·5 cm by the end of the second year of life.

(*f*) *Adult growth before* 1941 *and changes in* 1941

Since the experiment to reduce the population of perch began in 1941, data on the growth before the summer of 1941 can be considered as a basis with which subsequent changes in growth may be compared. As no collections of opercular were made before 1942, data on growth before 1941 have to be based entirely on back-calculations from older fish. The material from the Green Tuft trapping has

Table 9. *Mean lengths-for-age of year-classes of female perch before* 1941

Year-class	Number of fish	Age 1	2	3	4	5	6	7	8
Green Tuft trapped data									
1935	6	7·25	11·17	13·25	13·92	14·42	15·42	–	–
1936	11	7·07	11·25	12·91	13·93	14·80	–	–	–
1937	16	6·94	10·78	13·00	14·59	–	–	–	–
1938	17	6·60	11·10	13·81	–	–	–	–	–
Other data									
1933	2	6·90	11·85	14·25	15·50	15·95	16·35	16·90	17·45
1934	8	8·25	12·27	14·18	14·69	15·26	15·87	16·34	–
1935	37	7·62	11·72	13·67	14·58	15·16	15·64		
1936	68	7·55	11·61	13·55	14·35	15·04	–		
1937	96	7·31	11·50	13·45	14·65	–	–	–	–
1938	44	7·23	11·06	13·79	–	–	–	–	–

been supplemented by fish caught in traps in the winter of 1942 and 1943 and also the older fish caught by angling. These older trapped fish are the survivors of a heavy fishing mortality in 1941 and 1942 and may include an undue proportion of slow-growing fish. Conversely angling may have tended to select faster-growing fish, and this is probably the cause of the differences between the two sets of data

Table 10. *Combined data on growth before* 1941

	Age 1	2	3	4	5	6	7
Males							
Number of fish	24	24	24	19	11	6	–
Sum of increments in mean length	6·99	11·38	13·07	13·95	14·62	15·20	–
Calculated weight	2·80	13·8	21·8	26·9	31·3	35·7	–
Weight increment	2·80	11·0	8·0	5·1	4·4	4·4	–
Females							
Number of fish	305	305	305	244	132	53	10
Sum of increments in mean length	7·34	11·44	13·56	14·58	15·24	15·79	16·28
Calculated weight	3·17	14·8	24·4	30·9	36·1	40·3	44·8
Weight increment	3·17	11·6	9·6	6·5	6·2	4·2	4·5

shown in Table 9. The average growth-rate may thus be fairly accurately represented by the combination of data from all sources shown in Table 10. The operculars from many of these fish were difficult to read, partly because the fish were old and slow-growing and partly because the bones were stored for a long

time before cleaning. All the opercula were, however, read more than once with extra care, and the high age obtained for some of the fish in spite of their small size corresponds to a reasonable expectation of age distribution and natural and fishing mortalities. The data in Tables 9 and 10 and Figs. 1 and 2 show that before 1941 annual increment in weight was at a maximum in the second and third years

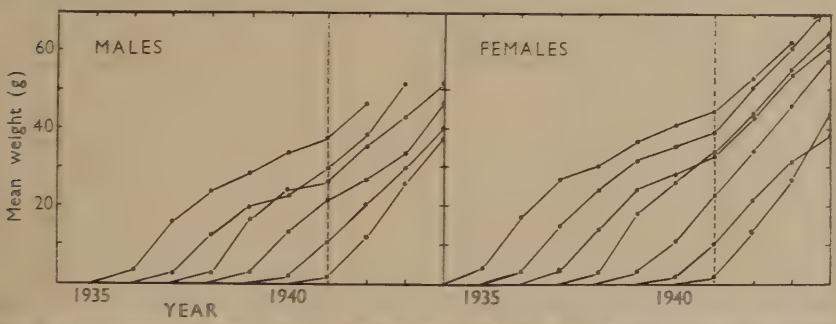

Fig. 10. Growth-curves for weight against age for male and female fish of the year-classes before 1941, to show the increase in growth-rate in 1941. The data have been adjusted for temperature variations.

of life and then declined in the fourth and fifth years. Thereafter it was fairly constant, though the data are not adequate to say whether or not the growth-rate eventually declined as a maximum size was approached.

Table 11. *Annual increments in weight adjusted for temperature*

Data for adult perch of successive year-classes in the periods before and after 1941.

Year-class	1937	1938	1939	1940	1941	1942	1943	1944
MALES								
1935	7·8	4·7	5·4	3·7	9·2	–	–	–
1936		7·2	3·8	3·3	8·6	7·8	8·6	–
1937			7·4	6·0	8·6	13·0	–	–
1938				7·9	5·6	6·7	13·6	–
1939					9·7	9·4	10·3	7·9
Averages	7·8	5·9	5·5	5·2	8·3	9·2	10·8	7·9
Grand averages			5·7				9·2	
FEMALES								
1934	3·4	6·4	3·9	3·9	8·5	9·7	–	–
1935		7·8	3·5	3·7	11·9	10·3	11·3	–
1936			3·9	4·7	9·8	11·2	8·3	7·0
1937				6·8	10·8	11·4	9·9	–
1938					11·2	12·0	11·7	13·2
Averages	3·4	7·1	3·8	4·8	10·4	10·9	10·3	10·1
Grand averages			4·8				10·5	

The weight increments have been adjusted for temperature differences and are shown in Table 11 together with similar data for adult fish from 1941 to 1944. It will be seen from this table and from the growth curves for weight in Fig. 10 that the average annual weight increment in the years immediately preceding 1941

was about 5 g, the data for males showing in this analysis a slightly higher rate than those for the females due to the inclusion of II-group fish. In 1941, however, there was a sharp increase to 8·3 g for males and 10·4 g for females; similar rates were shown for the same year-classes in the three subsequent years and the usual decline in growth in the third and fourth years no longer occurred (Fig. 10). The operculars of these fish showed quite clearly the sharp change in the width of the summer zones in 1941, and there is little doubt that a considerable increase in growth-rate occurred in that year, even if the difficulties of interpreting the inner rings of the operculars detract from the accuracy of the exact calculation of the rate of growth before 1941.

The trap fishery started on a large and intensive scale in the spring of 1941 and the catches made in the trials of 1940, in 1941 and in 1942 and subsequent years show that a reduction in the population of adult perch of the order of 45% had occurred by the end of the trapping season in 1941 which is the beginning of the growing season (Table 13 and Fig. 12). Similar reductions occurred in the next two years but no similar increases in growth occurred after 1941 to the fish already adult before then.

(*g*) *Adult growth since* 1941 *and its relationship to changes in population density*

The increase in growth-rate shown by all adult perch in the summer of 1941 has been discussed in the previous section. The year-classes already adult in 1941 showed no subsequent changes in growth and their annual increment in weight remained fairly constant throughout the rest of their life at a rate of about 9 g for males and 10 g for females. The year-classes becoming adult in 1941 and 1942 adopted similar arithmetic rates of growth that were maintained throughout life. The main feature of adult growth after 1941, however, was the gradual but steady increase in the rate of growth shown by each successive year-class as it became adult in its third and fourth year. This change is clearly shown in the average annual increment listed in Table 12 and graphed in Fig. 11. It will also be seen that the rate of increase in increment has been remarkably constant but exponential. The logarithms of the average annual increments for each sex, when plotted against year-class, lie very close to a straight line, and regressions were calculated by the method of least squares. The formulae for these are:

$$\text{males: } y = 0{\cdot}829 + 0{\cdot}0420x \text{ (S.E.}b = 0{\cdot}0084)$$
$$\text{females: } y = 0{\cdot}898 + 0{\cdot}0462x \text{ (S.E.}b = 0{\cdot}0119)$$

where y = logarithm of average annual increment in weight and x = year-class with 1936 = 0. Correlation coefficients calculated for the same data gave values of r of 0·992 for males and 0·970 for females. It is clear from these values of r and from an inspection of Fig. 11 that agreement with the regression lines is remarkably good, though the points for one or two of the female year-classes (*e.g.* 1946 and 1950) where the averages were based on very few fish lie some way off the line. The regression coefficient b for females is slightly but not significantly greater than that for males, but as the females grew faster than the males in 1941 the

Table 12. *Data on density and growth of year-classes*

Estimates of density of year-classes as laid eggs and when III (based on catches of spawning females and three- and four-year-old fish in the traps), growth (adjusted for temperature) in the first and second years, and average growth when adult (adjusted for temperature).

Year-class	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953
Relative number of eggs laid (% of 1941)								100	103	59	33	33	31	25	24	19	24	17	16	–
Relative number of fish when III (% of 1940)							100	98	57	68	51	38	1·0	6·8	0·8	50	3·8	13	7·2	–
Weight increment in first year (g)							1·9	1·5	2·3	2·6	2·4	2·0	2·4	2·4	2·2	3·4	2·1	2·4	2·2	–
Weight increment in second year (g)							11·0	12·9	12·2	12·8	12·0	12·3	12·6	14·5	18·1	12·6	16·2	13·2	11·8	–
Average annual weight increment when adult (g):																				
MALES																				
Before 1941	–	5·4	4·8	6·7	7·9															
After 1941	–	9·2	8·3	10·8	8·6	9·4	10·9	10·3	10·8	13·4	14·3	16·0	18·2	20·9	20·9	23·0	26·7	28·2	30·4	37·1
FEMALES																				
Before 1941	4·4	5·0	4·3	6·8																
After 1941	9·1	11·2	9·1	10·8	10·9	10·0	12·6	13·7	15·0	16·6	19·0	22·0	17·5	28·5	–	30·0	29·0	42·0	52·0	–

Table 13. *Estimates of the relative number and biomass population densities for adult perch in successive summers*

Based on the geometric means of catches-per-trap in the preceding and following trapping seasons and expressed as percentages of the 1940 values.

	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955
Number of adults	100	56	31	15	12	12	8·3	5·8	3·8	2·2	3·2	3·8	3·2	3·0	2·3	2·2
Total biomass of adults	100	58	31	16	13	14	11	9·3	7·7	6·5	7·1	7·1	9·2	10	8·9	8·6
Biomass of fish 13-18 cm	100	53	25	13	11	10	7·7	7·2	5·1	2·4	1·6	2·9	4·0	2·1	1·5	0·5
Biomass of fish over 18 cm	100	57	22	10	20	59	78	96	125	175	216	173	225	336	308	331

relative difference has been maintained and the actual difference between the sexes becomes more apparent. Although the increases in growth-rate were at first slight, by 1955 the youngest adult fish were adding to their weight each year an increment 6-10 times that usual before 1941 and 3-5 times that of adult fish in 1941.

The only known change in ecological conditions in Windermere that could account for these marked changes in growth-rate is the change in the population density of the perch produced by the trap fishery. The best measure of abundance or population density is provided by the statistics of the catches in the traps

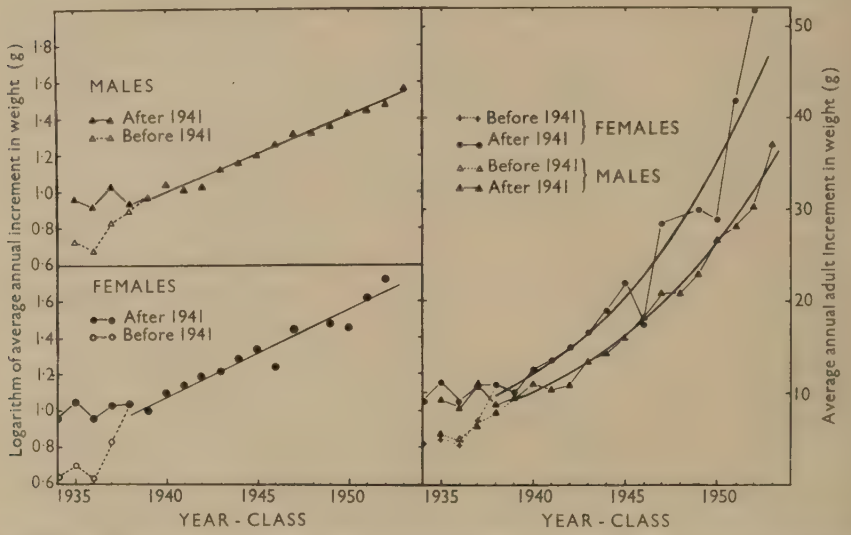

Fig. 11. Left, the logarithms of the average annual increment in weight made by male and female adult fish of successive year-classes. For the early year-classes points are plotted for growth before and growth after 1941. The straight lines are the least-squares regressions for year-classes 1939-53 for males and 1938-52 for females.

Right, the same data plotted on an arithmetic scale. The curves are the logarithmic regressions of the left-hand figures.

themselves. As each short trapping season itself reduces the population density the most satisfactory measure of abundance in the summer growing season is provided by the geometric mean of the catches per trap in the preceding and following trapping seasons. Such geometric means are tabulated in Table 13 and graphed in Fig. 12. The figure for 1940, representing the population desnity before the start of the trapping, is derived from the geometric mean of the catches in the trial year of 1940 when no significant population reduction occurred, and 1941, the first year of large-scale trapping. There is evidence that the vulnerability of the perch to the traps varies somewhat from year to year but this can and has been allowed for on a basis of catches over a series of years. No other comparable data on abundance are available but records of catches in seines and other gear indicate that the trap catches give a good relative measure of the abundance of adult perch and that no large group of perch has been missed by the trap fishery.

Table 13 and Fig. 12 show that from 1941 to 1944 each season's trapping reduced the population at the rate of about 45% a year. After 1944 the rate of decrease was less and from 1948 onwards the population density remained relatively constant. These data represent numbers of perch, but as any effect upon food supply might be more closely related to total weight or biomass density, data on biomass have been calculated and added to Table 13 and Fig. 12. This shows that although initially the reduction in biomass density was greater than the reduction

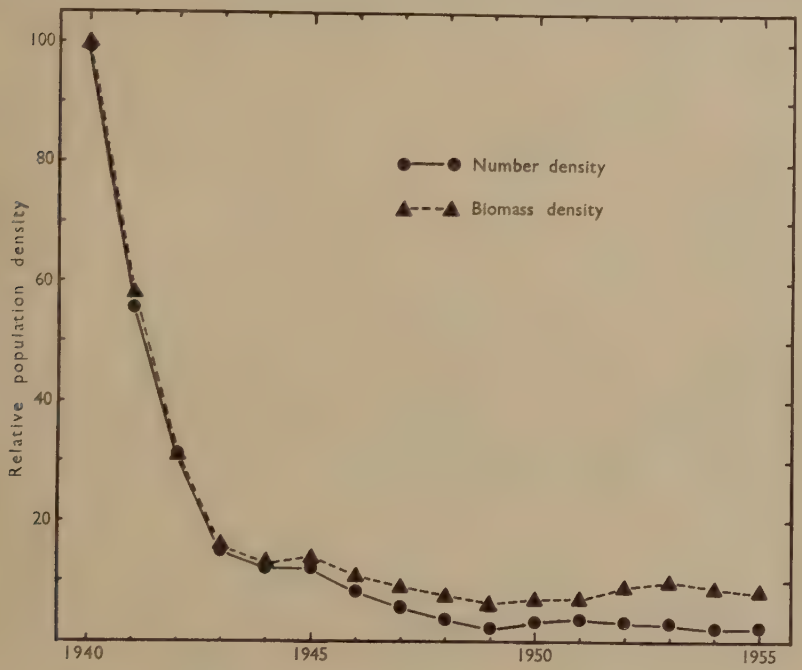

Fig. 12. Changes in population density. The geometric means of the catches per trap made in successive pairs of years from 1940 - 1941 to 1955 - 1956 expressed as a percentage of the 1940-41 value. The mean for each pair is plotted against the first year as indicating the population density in the summer growing season immediately following the trapping season.

in number density, in the later years the changes in growth-rate and age-composition modified this. Since 1948 the average number density has been about 3% of that in 1940 but the biomass density about 8% of that in 1940.

It seemed obvious to attempt to relate the changes in growth-rate with the fall in population density and so a number of correlation coefficients were calculated for various measures of growth and population density, bearing in mind that there might be a lag in the effect of population changes and also that the third and fourth year of life appeared to be crucial in fixing subsequent adult growth-rate. Measures of growth tested included the logarithm of the average adult annual increment in weight for males and females, the logarithmic growth-rate in the third and

fourth years, and an average k for the von Bertalanffy growth formula for the second to fifth years of life (Beverton & Holt 1958). Measures of population density tested included number density in first, second, third and fourth years of life, and various sums of these up to the sum over the five year period from −1 to +4 years of life, the density of fish of the same age only in the third and fourth year, and various sums of biomass density in early years of life. Nearly all of these gave highly significant negative values of r, up to a maximum of −0·947 for the correlation between the logarithm of the average annual increment and the sum of the number density over a five year period. The type of relationship obtained is shown in Fig. 13.

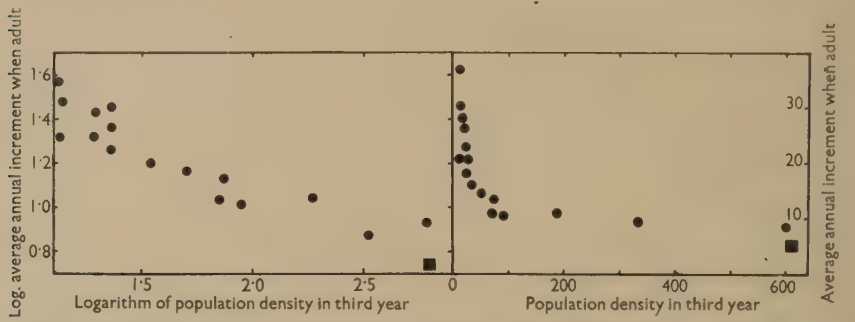

Fig. 13. Adult growth and population density. The average annual weight increments when adult for male fish of successive year-classes plotted against estimates (from catches per unit-effort in traps) of the density of the whole adult population when each year-class was in its third year. The left-hand graph has logarithmic scales, the right-hand arithmetic. The large square represents the growth before 1941 and the 1940 population density.

None of these correlation coefficients had as large a value, however, as those obtained for the relationships between growth and time as measured by successive year-classes or years of the experiment. The calculation of partial regression coefficients between growth, population density and year showed clearly that while there was a high degree of correlation between growth and year on the one hand, and often population density and year on the other, there was no real correlation between growth and population density. For example, the partial correlation coefficient for the logarithm of average adult annual increment and year = +0·826 (which is highly significant) but the corresponding coefficient for the logarithm of average adult annual increment and the logarithm of population density when the fish were II and III = −0·195 (which is quite non-significant). Similar values for r were obtained for other measures of adult growth and population density when the effect of year was eliminated. This conclusion that the relationship between population density and growth is not direct, nor continuous through the period under observation, is supported by the continued steady increase in growth-rate shown by successive year-classes in the latter years (Fig. 11), while there was no corresponding further decrease in number or biomass density of fish (Fig. 12).

It seems likely that the effect of the initial and considerable reduction in popula-

tion density was an immediate stimulus to faster growth in 1941, but that after that the pressure of population density was no longer a factor limiting growth-rate. The subsequent gradual increase in growth-rate shown by successive broods of young adult fish might reflect a gradual increase in the population density of benthic food organisms. Such animals might be expected to increase their numbers rather slowly and the exponential form of the increase in perch growth-rate might be a reflection of an unrestricted benthic fauna population increasing in the usual

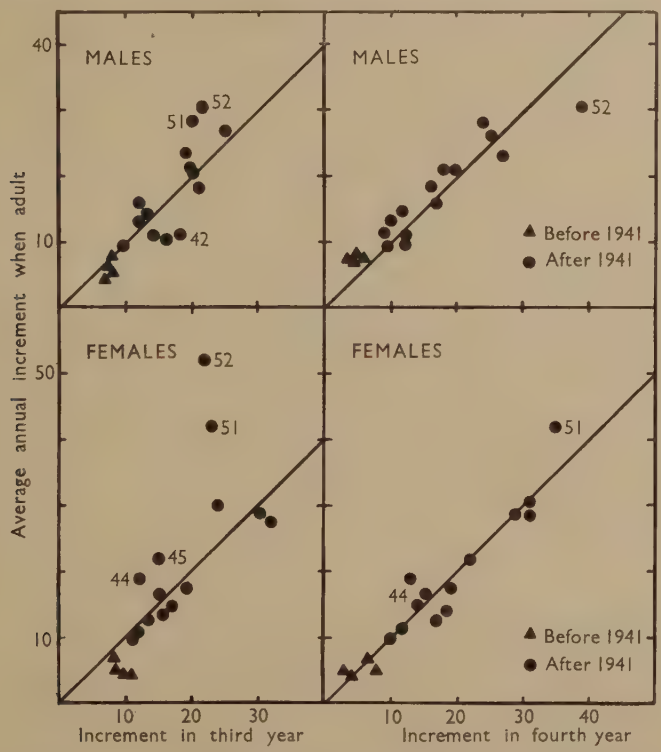

Fig. 14. Correlations between growth in the third and fourth years and adult growth. Average annual increment in weight when adult plotted against the weight increment in the third year (when II) and fourth year (when III) for males and females.

exponential fashion. Unfortunately there are no data available with which to make any assessment of changes in the density or rates of production of the food organisms of perch. In any case the scale of any such investigation and the inadequacy of sampling methods would probably be prohibitive.

In the preceding discussion the apparent importance of the growth made in the third and fourth years of life, and the constancy of the arithmetic growth in subsequent years has been stressed. Plots of average annual increment when adult against increment in the third and fourth years for male and female year-classes (Fig. 14) showed that since 1941 the average adult increment has been very

similar to the increment in the third year of life. Before 1941 average adult growth-rate tended to be less than that in the third year, though almost identical with that in the fourth year. The most recent year-classes, those of 1951 and 1952, tended to increase their growth-rate after the third year, especially in the case of the females. It is not yet possible to say whether the growth of subsequent year-classes will continue to show this trend. On the whole, however, it can be concluded that the arithmetic growth-rate of the male fish is determined for adult life in the third year and for female fish largely determined in the third year and quite determined in the fourth year.

As noted in the previous section on the effects of temperature there is some variation in growth-rate from year to year not accounted for by temperature fluctuations. The year-classes that have been observed over a number of years, however, have maintained a remarkably constant arithmetic growth as can be seen from Table 7 and Figs. 1 and 2. There is a suggestion that some of the very old fish may, however, be slowing down in growth. For example, the increment made by the female fish of the 1940 and 1941 year-classes was considerably less than the average in their last year of observation. The numbers of fish of these ages available, however, is too small for any certain conclusion to be drawn. It is possible that the constant arithmetic growth is an artefact of the falling population density and under normal conditions the growth-rate would tend to decline, but the evidence available on growth before 1941 suggests that there was little tendency for a declining adult growth-rate even under those conditions though the data available from old fish are too scanty to be sure of this.

Beverton & Holt (1958) have found that the growth of most fish can be readily described by a formula of the von Bertalanffy type where the growth-rate declines as the fish approaches an ultimate maximum size. Attempts have been made to use this useful formula for Windermere perch but as Fig. 4 shows, even before 1941 the graph of length at age $x+1$ plotted against length at age x (Ford 1933, Walford 1946) tends to curve away to a slope roughly parallel to the 45° line after three or four years. Thus only for the first two or three years is the von Bertalanffy type of growth followed, and then only approximately. It is possible that the changes in diet with increase in size account for this (Allen 1935).

(*h*) *Changes in size, fecundity and food resulting from changes in growth-rate*

The average size of any group of fish is determined both by their average age and their growth-rate. It is of interest, however, to examine the changes in size that have occurred among the perch in Windermere in order to observe the effect of the changes in growth-rate since 1941. Average weights of male and female perch caught in the traps at Green Tuft each year and measured are plotted in Fig. 15. The mean weight of a series of samples of perch trapped in the autumn of 1939 is also shown. This mean weight of 24·2 g is probably the best measure available of the average weight of adult perch before 1941. Some of the changes shown by these two graphs are due to changes in age-composition. For example the onset of

large-scale trapping immediately lowered the average age; this is reflected in the fall in average size from 1940 to 1943. Similarly the sharp fall in average size in the males in 1951 and in the females in 1952 is due to the recruitment of the exceptionally strong 1949 year-class.

Data on average weight are also plotted for an incomplete series of catches made by angling with a minnow as bait in the autumn. Most of these samples came from the Millerground Hill area of Windermere, which is a favourite site for perch

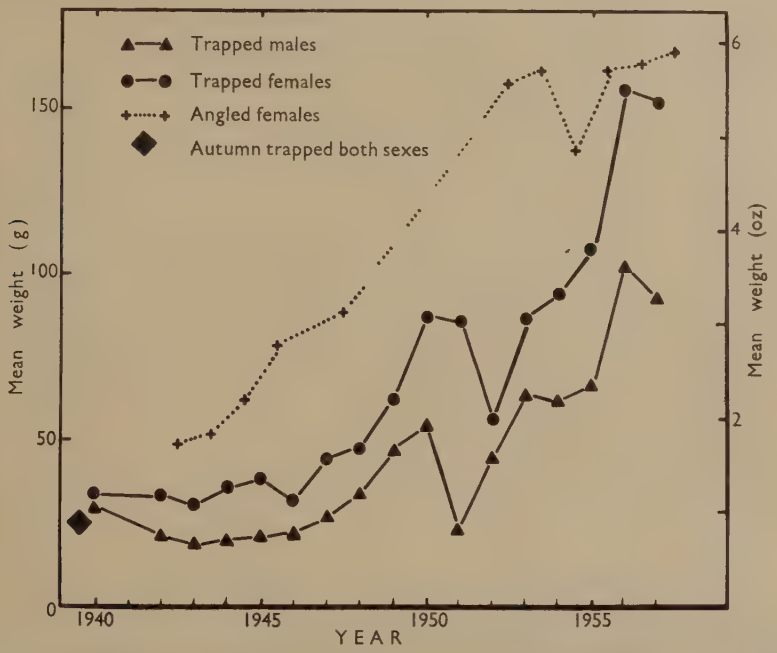

Fig. 15. Changes in average size. The mean weight of the trapped male and female fish for successive seasons from 1940 to 1957. Also the mean weight of the female fish in a series of samples angled in the autumn, and both sexes in a sample trapped in the autumn of 1939.

angling in October. Nearly all the perch caught by such angling are females and the rare males have been omitted from these samples.

Both these sets of data show an approximate three-fold increase in average weight from 1940 to 1957. The means of trapped fish indicate roughly the average size of the adult perch, the means of angled fish the average size of a selected sample of the largest sized perch among the general population. At any time throughout the period of observation any one sample of perch, especially if angled, has tended to be distributed normally in length. This is because, as well as the usual individual variation in growth-rate, the faster growth of each successive year-class has caused the largest fish to consist of a mixture of all adult ages and growth-rates ranging from young fast-growing fish to very old slow-growing fish.

No samples of angled perch are available for the period before 1941, but from the statements of older anglers it is apparent that before 1941 when the perch population was really dense, skilful or lucky selection of the site for angling could yield catches of perch averaging about 100 g in weight though the normal size caught was less than this. It would probably be correct to conclude that the average size of the angled perch in Windermere has increased from 1940 to 1957 about 2½ times from 65 g to 170 g or from 2¼ oz to 6 oz.

The increase in size in the adult female perch has been accompanied by a corresponding increase in fecundity. Gonad-weights and egg-counts from samples of ripe female perch showed that there was a direct proportion between body-weight and gonad-weight (Le Cren 1951), and that egg numbers were roughly proportional to gonad weights. Thus the approximate three-fold increase in the average weight of the female perch has been accompanied by a three-fold increase in individual fecundity. The population density of female perch was in 1956 about 6% of its level in 1940, so the increase in fecundity due to increase in growth-rate has only partially compensated for the reduction in the numbers of spawning fish.

The marked changes in size-distribution concurrently with changes in abundance have also probably resulted in changes in the intensity of feeding by the perch on different types of food. Allen (1935) investigated the food of perch in Windermere and found that up to a length of 13 cm plankton formed more than half the diet, from 13 cm to about 18 cm benthic invertebrates formed more than half the food, and over 18 cm in length the perch fed mainly on small fish. There was considerable overlap between these three categories, and in winter, when the rate of feeding was much less, plankton predominated in the diet of fish of all sizes. As a first approximation, however, division of the perch into three size-groups, <13 cm, 13-18, and >18 cm, will divide the population into perch the bulk of whose food consists of plankton, benthos and fish respectively. The catches of perch <13 cm in traps do not adequately measure the density of plankton-feeding fish as immature females are not caught in any numbers and much more plankton will be eaten by 0-group perch than I- and II-group fish. The biomass density of benthos-feeding and fish-feeding perch has, however, been calculated from the catches per trap, the size distribution from measured samples, and the length-weight relationship (Table 13 and Fig. 16). The early samples trapped in 1940 and 1942 do not give a very adequate idea of the density of perch over 18 cm in length as few females were caught or measured, but a series of small samples caught in the autumns of 1939 and 1942 give some additional data. It is clear, however, that nearly all the biomass of perch over 13 cm in length fed on bottom fauna, and only from 3-6% were fish-feeding. The marked reduction in the numbers of older fish in 1941 and 1942 reduced still further the proportion and total weight of fish-feeding perch, but after 1943 the changes in growth-rate began to increase the proportion of larger perch. The total biomass of adult (or trapped sized) perch has remained relatively constant since 1948 at about 7-9% of the 1940 level (Fig. 12), but the biomass of benthos-feeding perch continued to fall until by 1955 it was only about 0·5% of its level in 1940. The biomass of fish-feeding perch,

however, continued to rise; by about 1949 it was equal to its 1940 level and by 1953-55 had reached a level about 2½ times that in 1940 before the trapping experiment began. The rapid growth of perch through the benthos-feeding stage in the later years thus means that the reduction in intensity of feeding on benthos was considerably more than that indicated by the fall in total catches. On the other hand the intensity of feeding on fish is probably two or three times what it was before the experiment started, in spite of the great reduction in total numbers. Although the biomass of a fish population probably gives a better measure of intensity of feeding than does number density, estimates of the changes in numbers

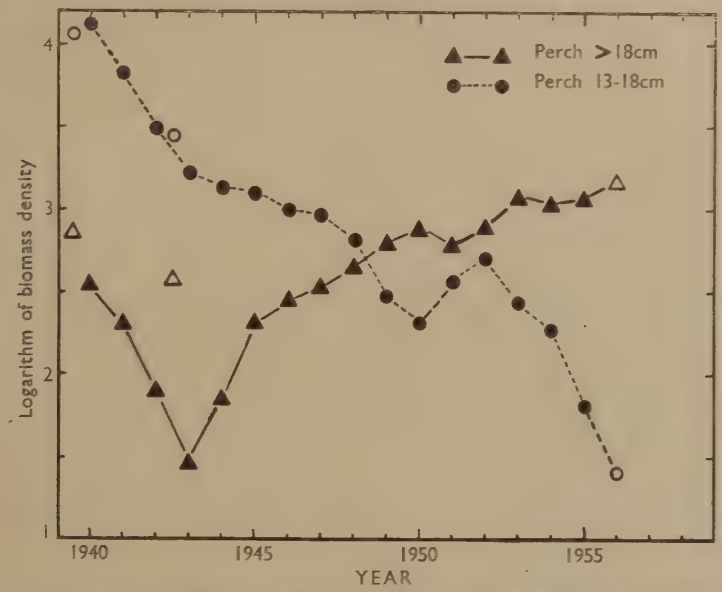

Fig. 16. The changes in population density of perch feeding on benthos and fish respectively. The logarithm of relative biomass density (estimated from trap catches) for successive years from 1940 to 1956. The open circles and triangles for 1939 and 1942 are based on autumn trapped samples unselected for sex. The 1956 points are provisional estimates.

of perch in the respective feeding categories give similar results. The total numbers of fish-feeding perch in Windermere in 1953-56 were probably about twice as many as in 1940.

These rough estimates of the changes in the proportions and biomass of perch feeding on different foods presuppose that there have been no marked changes in feeding habits since 1935. No detailed study of perch food has been made since then, but a few stomachs were examined, and they gave no evidence of any change since Allen's investigation.

(*i*) *The growth of perch in Windermere compared to other waters*

It is of interest to compare the growth-rates in 1940 and 1956 with those found for the perch elsewhere. A number of growth-rates for very slow-growing,

'stunted' perch populations have been published, among which that found for Abborrtjärn II by Alm (1946) is one of the slowest. The fastest published growth of perch that I have found is that of the Bodensee published by Haakh (1929). These growth-curves have been plotted in Fig. 17 together with curves for Windermere before 1941 and for two representative subsequent year-classes. The only other published data for British waters (Hartley 1947) and the curve for Längelmäväsi in Finland (Brofeldt 1917 corrected by Segerstråle 1933) are also included.

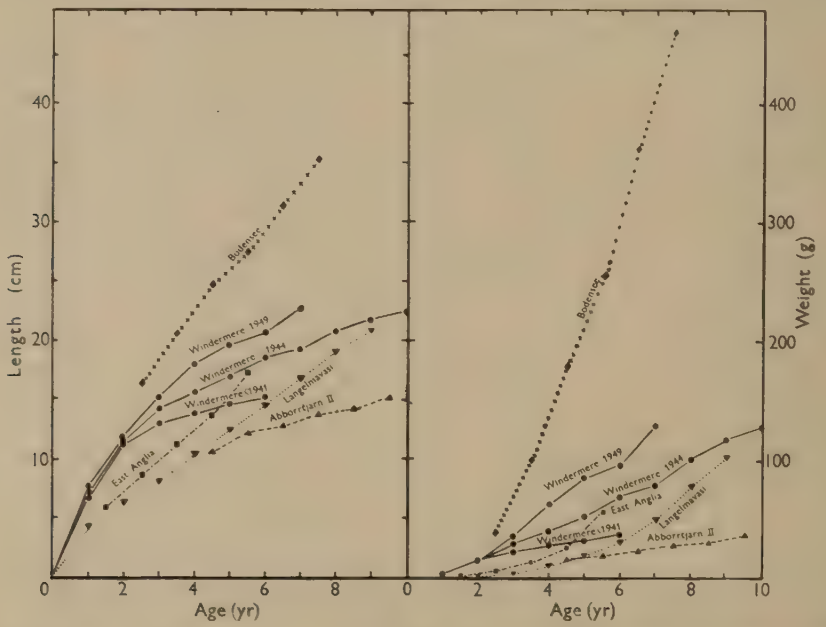

Fig. 17. The growth of perch in various waters. Length for age (left-hand graph) and weight for age (right-hand graph) for males of the combined year-classes before 1941, and the 1944 and 1949 year-classes plotted for comparison with data from East Anglia (Hartley 1947), Abborrtjärn II (Alm 1946), Längelmäväsi (Brofeldt 1917 and Segerstråle 1933) and Bodensee (Haakh 1929).

These data show that the early growth of Windermere perch has always been good, especially in comparison with typical Scandinavian waters of higher latitude such as Längelmäväsi. The rate of growth of the adults before 1941 was similar to that of other stunted populations such as that of Alm's Abborrtjärns, but the size of the Windermere perch was a little larger owing to better growth in the early years. The more recent year-classes (*e.g.* 1949) have been growing at a rate that is better than most published growth-rates, but not as fast as the perch of the Bodensee or one or two other waters in the north of Britain where the growth-rate is probably similar to that in the Bodensee (Le Cren, unpublished data). The increase in growth in Windermere with the reduction in population density is similar to that described by Alm (1946) for the perch in the Stora Holmtjärn after intensive fishing. In this latter lake, however, the response of the growth-rate

to population reduction was quicker, as the average length increased from about 15 cm to about 21 cm in only five years: this is equivalent to an approximate three-fold increase in average weight and is similar to that attained in Windermere in about fifteen years. It is clear that the fairly large oligotrophic north basin of Windermere belongs to Alm's first category of lakes which are capable of good perch growth provided the population is not too dense.

DISCUSSION AND CONCLUSIONS

The principal aim of the present investigation has been the identification of some of the more important factors influencing the growth of the perch, and the determination of at least some empirical relationships between growth-rate and factors that influence growth.

Some of the factors influencing the growth of the perch had already been investigated, and the wide variation in growth-rate possible (*e.g.* Fig. 17) had been established. The analysis of data collected over short time-intervals in a variety of waters can provide information on such features as age at onset of maturity in relation to growth-rate, differential growth of the two sexes and the correlation between lake-type and growth-rate. The elucidation of further features of the growth-rate, however, requires experimentation. Alm (1946) relied largely on experiments in ponds and small lakes carried out in considerable detail over a number of years and was able to increase our knowledge of perch growth very considerably. The present investigation has fallen between the pond experiments of Alm and the purely field observations of previous workers as it attempted to analyse the influence on growth of natural variations in some environmental factors and the large-scale experimental alteration of another factor, population density, over a period of about twenty years.

Many of the detailed results of the analysis of the Windermere data confirm or elaborate the findings of other workers. For example, it seems to be a feature of nearly all perch populations that the adult females grow slightly faster than the males. The males tend to mature when a year or more younger than the females and faster-growing individuals mature earlier than slow growers. Most of the published data also agree with the present data in the general form of perch growth. The growth in weight through most of adult life is remarkably constant and arithmetic, and produces straight line slopes of weight plotted against age even if growth is very fast or very slow (Fig. 17).

Temperature has been found to have an important influence on the growth of a number of fish species: both on experimental evidence (*e.g.* Brown 1946 on *Salmo trutta* Linn.) and on the observed correlations between variations in natural temperatures and growth-rates (*e.g.* Hile 1941 on *Amblioplites rupestris* (Rafinesque)). As far as I am aware no similar observations have previously been made on the relations between temperature and the growth of the perch. The present investigation has, however, revealed that temperature is of great importance in the growth of all ages of perch and that very considerable year-to-year variations

in growth can occur and can be largely attributed to temperature differences. It has also been possible to estimate simple empirical relationships between temperature and growth and this has made it possible to correct for one environmental factor and in this way increase the precision of the analysis of the effects of other factors. Although it is probable that temperature and other physical factors have an effect on the whole biota and thus on the food supply of the fish, it appears likely from the way all sizes of perch are similarly and rapidly affected and the simplicity of the empirical relationship between temperature and growth, that the effect is a direct one. This would, in general, be supported by experimental evidence on other species (*e.g.* Brown 1946) and by the similar year-to-year variations in growth found in different lakes in the same region (*e.g.* Hile 1941).

The other main growth-influencing factor revealed by the present investigation has been population density. The importance of population density in influencing the growth-rate of fish has long been recognized (*e.g.* Petersen 1894, Dahl 1917) but the exact relationships between numbers and growth and the role of the food organisms are obviously complex and still poorly understood.

The present experimental reduction in perch population density has shown that density has no effect on first-year growth and little effect on second-year growth. These findings in general support the results of Alm's pond experiments where there was little correlation between density and first-year growth but more correlation in the second-year. The perch feeds largely on plankton or littoral weed-living Entomostraca in the first year and much of the second year of life (Allen 1935, Smyly 1952) and this suggests that the density of plankton and Entomostraca is not significantly influenced by the density of fish feeding on it. Smyly (1952) found that food sometimes appeared to be short for perch fry in Windermere, but that this shortage seemed to be due to gaps between the population maxima of successive entomostracan species rather than to the effect of the perch fry themselves on the numbers of their prey. Smyly also found that the perch fry tended to feed on bottom fauna such as chironomid larvae or on smaller fry when entomostracan food was scarce. The observations on *Oncorhynchus nerka* Walbaum made by Ricker & Foerster suggest that in some species and waters the feeding of freshwater fish can have a significant effect on planktonic prey species and thus on the growth-rate of the fish (Foerster 1943, Ricker & Foerster 1948), but in general the relationship between predator and prey population densities are perhaps less close for fish feeding on plankton than for fish feeding on bottom fauna.

One of the interesting results of the observations on the growth of adult perch has been the tendency for the growth of any one year-class to be constant and arithmetic after the third year of life. This emphasizes the importance of the third and fourth years of life in the growth of the perch. The reduction of population density to about half in 1941 was, however, a sufficient stimulus to increase the growth-rate of the remaining adult perch. The stimulus provided by transplantation to a new, perch-free environment in Alm's experiments (Alm 1946, pp. 81-4) had a similar effect upon the growth-rate of those perch. The further reductions in population density in 1942 and 1943 had no further effect on the

growth-rate of fish already adult: perhaps these further stimuli were not adequate to induce further increases in a growth-rate normally fixed and stable by this age.

It is possible that the subsequent increases in growth-rate shown by successive year-classes of young adults could be due to the selection of genetically faster growing strains by the changed conditions in the lake. On the other hand a genetical change of this kind would seem unlikely. Alm (1946) has shown that the growth-rate of perch is little influenced by genetical factors, and that populations that have been very stunted for a long period have as good intrinsic powers of growth under favourable conditions as have perch from fast-growing populations. The heaviest mortality, and thus selection, occurs in the fry stages whose growth appears to have been unaffected by the changes in population density. Further, the correlation between faster juvenile growth and earlier maturity means that the trap fishery tended to impose a heavier fishing mortality on faster-growing individuals and thus favour for survival the rather slower-growing fish.

The most likely cause of the increase in growth-rate in the third and fourth and subsequent years of life is that there has been an increase in the food supply for perch of that size. Perch in their third year feed roughly equally on larger plankton and bottom fauna and in the fourth year largely on bottom fauna, though in the later years of the experiment by the end of the fourth year many of the perch will have passed through the benthos-feeding stage and will have been feeding largely on fish. The main benthic animals in the diet were recorded by Allen (1935) as *Gammarus*, chironomid larvae and pupae, *Sialis* larvae and *Ephemera* nymphs: the larvae and nymphs of other aquatic insects and leeches are also eaten by perch between 13 and 18 cm in length.

The bulk of the food of the adult population before 1941 consisted of these benthic animals (Fig. 16) and the changes in population-density and growth-rate resulted in a reduction to about 0·5 %, in the biomass of benthos-feeding perch. Approximate estimates of the benthos consumed, based on dividing the food required into that needed for maintenance and that used for growth shows that the perch probably ate in 1956 about 1 % of the benthos that they ate in 1940. An increase in the amount of benthic food adequate to explain the increases in growth-rate is therefore very likely, and some further discussion is justified even though lack of basic knowledge of the population dynamics of benthic animals must make it largely conjectural.

Beverton & Holt (1958) have discussed the grazing of benthos by fish, and attempted a theoretical analysis. They emphasize its analogies with the exploitation of fish stocks by a fishery and consider that for marine benthos at least, the effect of the grazing will be confined largely to changing the survival-rate of the organisms and not their rate of recruitment. In fresh water, however, there may be some long-term effects on the rates of reproduction and recruitment, as the fecundity of fresh water animals is usually much lower, and there are no pelagic larval stages. The only direct measurement of the effect of the grazing of fish on fresh water benthos of which I am aware is the experiment of Ball & Hayne (1952). They removed the whole fish population from a small lake and observed a threefold

increase in density of benthos within a year. Hynes (1955) and Macan & Mackereth (1957) have shown that *Gammarus* can have several generations in a season and Hynes estimates that one female *Gammarus* might give rise to 300 off-spring in a year. Mann (1957) has published life-cycle and fecundity data for leeches such as *Erpodbella*, and it appears that they would not be capable of as high a rate of reproductive increase as *Gammarus*.

The rate of feeding and thus growth-rate in a fish such as the perch is presumably normally limited by the density of available food organisms. Observations in aquaria and on the kinds of animals eaten by perch show that it feeds by sight on moving prey, and the available food will thus consist of those prey animals that are swimming exposed. The density of these animals may bear little direct relationship to their total density, as most individuals will spend most of their time under the cover of stones, weeds, etc. Macan & Mackereth (1957) make the interesting suggestion that, as the population of *Gammarus* under cover increases, the resultant jostling stimulates more individuals to wander off and leave their cover. Such a behaviour might be very relevant to the number available to feeding perch.

The two main features of the increase in perch growth-rate are the immediate increase in 1941 after the initial reduction in population, and the gradual but exponential increase in the growth-rate of the young adults of successive year-classes. These would suggest that the increase in density of available benthos had taken place in two stages: firstly an immediate increase in density perhaps due only to an increase in the survival-rate of the benthos already present in June 1941, and secondly a much more gradual increase in abundance due largely to a gradually increasing rate of recruitment. The latter may at first have given rise to only a small increase in benthos available to feeding perch while the niches under cover became filled: later, as the population pressure under cover increased, a greater proportion of the animals might have been driven to leave the cover and thus become available to be eaten. These conjectures are not, however, entirely satisfactory, as it is strange that the initial increase in growth-rate in 1941 affected the older adults more than the younger ones, who hardly increased their growth at all, and that this initial increase was not followed by any further significant increase for some while. Perhaps the initial increase in growth-rate was caused by some social influences within the perch population itself. Whatever the exact explanation of the change in growth-rate, the gradual, but steady and exponential form of the increase, apparently independent of changes in perch population density after 1941, and the considerable increase achieved by 1956 remain the outstanding results of the experiment.

The adult growth-rate of new year-classes was still increasing in 1955-56, and it is pertinent to speculate on the level of equilibrium growth-rate that may eventually be achieved. The estimate that the 1956 rate of feeding on benthos is only 1% of that in 1940 suggests that with the present population density the growth-rate would not be limited by supply of benthic food until it was very much faster. Although, as it becomes denser the benthos might provide enough food for rather larger sized perch so that the 18 cm length for the change to fish diet might

increase, it is probable that the supply of small fish as food for larger perch is much more likely to become the limiting factor. The 1956 perch population was probably eating between two and three times the weight of fish that was eaten by perch in 1940 (Fig. 19). It is also likely that the numbers of young perch have decreased (Table 12), but there are no quantitative data from which to estimate changes in the minnow and stickleback populations. Competition from the pike for small fish is likely to have increased, as in spite of the gill-net fishery for larger pike (Worthington 1949) the population of small pike was at least as abundant in the period 1949-56 as in 1941-43.

Finally there is the possibility that other species have increased to take the place of the perch. Accurate data on the numbers of trout, eels and char are difficult to obtain. Both the char and the trout have almost certainly increased in abundance since the reduction in numbers of larger pike (Worthington 1949; Frost 1954). The char feeds mostly in the open water on zooplankton and is unlikely to compete for food with the perch, but the diets of the trout and perch do overlap to a considerable extent (Frost 1946). Before 1941 the trout population was very small in relation to the perch population, probably less than 1% in biomass. It probably increased from 1944-55 about five times (Frost 1954) but is still almost certainly less than the biomass of perch, though it is possible that the trout now eats more benthos than does the perch. It is unlikely that the trout will increase in abundance much more, as its numbers depend partly on the spawning facilities in different streams.

The growth-rates of the young adult perch in 1956 are still less than those shown at some period of their life by the few exceptionally large individuals in Windermere who may add up to 200 g in weight in a year, or by the average perch in some other lakes in the district who have an annual weight increment of about 80 g a year (Le Cren, unpublished data). Some further increase in growth-rate is thus likely though it is improbable that the average annual increment will rise much above 100 g, or roughly twice the growth-rate of the youngest adults in 1955-56.

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In an investigation of this type extending over a period of years a large number of persons help in one way or another, and I have been fortunate in the wealth of assistance I have received, much of which I cannot specifically acknowledge. I am grateful to Mr G. J. Thompson and other members of the laboratory staff for their work in catching most of the perch examined, and to my colleagues Mrs K. McConnell, Dr K. R. Ashby, Mr W. J. P. Smyly, Mr P. H. T. Hartley and Miss C. Kipling for giving me considerable help in the collection of data. I am indebted to Dr E. B. Worthington and Mr J. H. Buchanan-Wollaston for guidance at the start of the investigation and Mr Wollaston, Dr Worthington and Dr H. B. N. Hynes have generously allowed me to make use of material and data collected by them. Most of the tedious calculation of means and tabulation of results was rapidly and accurately executed by Miss J. C. McCormack to whom I am especially grateful. I also wish to thank Mr H. C. Gilson, Miss C. Kipling and Mr F. T. K. Pentelow for their helpful comments on drafts of the manuscript.

SUMMARY

1. The opercular bones of perch collected mostly in traps from 1942-1956 are analysed for age and back-calculated growth to provide data on the growth of perch in Windermere and changes occurring from 1934 to 1956.

2. There was no sex difference in growth in the first and second year of life. Subsequently, female perch grew slightly faster than the males. Male and female perch that mature in their second and third years respectively were slightly larger at this age than those that matured later.

3. Considerable year-to-year variations occurred in growth at all ages, and these were correlated with variations in summer water temperature measured as degree-days over 14° C. Regressions of growth on temperature accounted for up to two-thirds of the year-to-year variation in growth.

4. The trap fishery started in 1941 reduced the dense population to about 13% of its original density by 1943, and thereafter at a slower rate. From 1949-55 the population remained relatively constant at about 3% of its density in 1940. Increases in growth-rate caused the biomass to fall to only about 8% of its 1940 density.

5. Before 1941, the perch in Windermere grew slowly; the adults having an annual weight increment of about 5 g. Perch adult in 1941 increased their growth sharply in 1941 after the first season of the fishery. These fish maintained a steady average increment of about 10 g in subsequent years in spite of further reductions in population density.

6. After 1941 each new year-class of perch showed increased growth-rate in its third and fourth year of life, which rate was maintained approximately constant in later years. The average annual increment in weight for adults of each year-class thus increased from about 10 g for the 1938 and 1939 year-classes to 52 g for the females of the 1952 year-class and 37 g for the males of the 1953 year-class. This increase closely followed an exponential curve and adult growth-rate was highly correlated with time from the start of the fishery but not with changes in population density after 1941.

7. Growth in the first two years of life remained relatively constant in spite of great fluctuations in population density of fry. Second-year growth was to some extent negatively correlated with the density of yearlings.

8. The changes in growth-rate resulted in approximate increases in the average weight of trapped perch from 30 g to 120 g and angled perch from 65 g to 170 g. The size increase also increased the number and biomass density of fish-feeding perch and decreased still further the density of benthos-feeders.

9. The implications of these results are discussed in relation to the literature on perch growth, the probable changes in benthos and other fish species in Windermere and forecasts of further changes in perch growth.

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THE DISTRIBUTION AND GROWTH OF *PROSIMULIUM* LARVAE (DIPTERA: SIMULIIDAE) IN HILL STREAMS IN NORTHERN ENGLAND

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(With 3 Figures in the Text)

The present work describes certain features of the altitudinal distribution and growth of the larvae of *Prosimulium hirtipes* Fries and *P. inflatum* Davies in hill streams in northern England. An explanation of the facts is presented, but it is recognized that since the information obtained is incomplete it must be regarded as no more than a working hypothesis.

The annual cycle of *P. hirtipes* (*sens. lat.*) is already well known. O'Kane (1926), working in New Hampshire, U.S.A., showed that larvae appeared in streams in the autumn and became fully grown by early spring when pupation occurred, adults emerging in April-May. Since eggs laid by these adults in May-June did not hatch until the autumn the species is apparently univoltine. Later workers (Twinn 1936, D. M. Davies 1950, Rubtzov 1956) have confirmed these observations. However, Rothfels (1956) has since shown that *P. hirtipes* in eastern Canada consists of at least two sibling species and L. Davies (1957) has produced anatomical evidence that the northern European *P. hirtipes* Fries as re-defined by Edwards (1915) and Puri (1925) is specifically distinct from the north American forms hitherto grouped under this name. The insect dealt with in this paper is the northern European form as found breeding in hill streams in Britain. Larvae of this species have been considered to be cold-water stenotherms, an idea based on their restriction to the colder months and to streams supposed to be relatively cold (Rubtzov 1940, Dorier & Freychet 1946, Grenier 1949). To test this hypothesis laboratory experiments were carried out on the effects of higher temperatures, and field observations were made on their seasonal development and on water temperatures in their natural environment.

SITES AND METHOD OF SAMPLING

Field work was carried out in 1954-57 on Crowdundle and Swindale Becks (Nat. grid refs. 35/6832, 35/7029) which drain the west slope of the main north Pennine ridge immediately south of Cross Fell and which flow eventually into the river Eden (see Table 1). Their sources lie at over 800 m altitude and their volume of flow is considerable even at 700 m, there being no indication of drying up in four seasons' work. The bed of both streams at all sampling points except those above

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650 m consists of loose stones 5-50 cm in length, with no rooted vegetation and negligible moss growth. Periodic collections were made at fixed points by lifting from five to thirty stones from broken-water sections of the streams, running the side of a finger across the larval masses and scraping them into a tube of alcohol.

Table 1. *Particulars of Crowdundle and Swindale Becks*

	Crowdundle		Swindale	
Km from source	Mean gradient	Width	Mean gradient	Width
0-1	1 in 6·9	*c.* 0·5 m	1 in 9·0	*c.* 0·5 m
1-2	1 in 4·7		1 in 6·2	
2-3	1 in 8·0	1-2 m	1 in 6·9	1-2 m
3-4	1 in 11·1		1 in 13·3	
4-5	1 in 28·5		1 in 20·0	
5-6	1 in 22·2	3-5 m	1 in 28·5	3-4 m
6-7	1 in 33·3		–	

This method ensures that very small individuals are obtained in roughly representative numbers. The object of the collections was to obtain sufficient larvae to determine approximately what proportion of the population at a particular point consisted of *P. hirtipes* and to determine the size distribution of the latter.

Occasional samples were obtained from other north Pennine streams, from streams in Caernarvonshire, Wales, the highlands of Scotland and the Lake District.

ALTITUDINAL DISTRIBUTION OF *PROSIMULIUM HIRTIPES* LARVAE

Once in each season larval samples were obtained from three to six stations from 180 to 800 m altitude, for two seasons in Crowdundle Beck and four seasons in Swindale Beck. The results are given with the stations grouped into two categories in Table 2. At the lower stations *P. hirtipes* was invariably present, often forming

Table 2. *Occurrence of* Prosimulium hirtipes *larvae above and below* 450 *m*

	180-450 m		450-800 m	
	Larvae	% *hirtipes*	Larvae	% *hirtipes*
Crowdundle Beck				
16 April 1954	611	13·2	284	0·7
14 April 1955	1063	21·3	35	0
Swindale Beck				
15 April 1954	429	61·5	626	3·3
23 April 1955	1160	46·5	148	0
23 March 1956	2721	37·5	269	0
22 November 1956	3316	1·1	924	0

20-50% of the total, while at the higher stations it was absent or present in very low numbers. All blackfly larvae were usually more sparse at the higher stations and samples taken above 450 m took from two to four times as long to collect as those below. Correlated with the rarity of *P. hirtipes* above 450 m there is evidence that within the range 180-450 m the proportion of its larvae tended to decrease as the upper limit was approached and this pattern was confirmed by repeated

sampling (Table 3). Swindale Beck in 1954 was an exception in this respect when *P. hirtipes* larvae appeared to be distributed higher up the stream than usual and to form an unusually high proportion of the total larvae in the lower parts.

In High Cup Gill, Ardale and Rundale Becks, also draining the west slope of the Pennine ridge, three samples out of four from below 450 m included *P. hirtipes*, while

Table 3. *Percentage of* Prosimulium hirtipes *larvae at different altitudes* (*sample sizes in parentheses*)

	Altitude (m)					
	180	300	400	430	600	630
Crowdundle Beck						
16 April 1954	17·3 (133)	*50·0 (60)	9·0 (170)	4·8 (248)		1·0 (115)
14 April 1955	22·3 (614)	*31·9 (238)	6·3 (142)	5·8 (69)	–	0 (28)
Swindale Beck						
15 April 1954	82·0 (106)	58·0 (143)	37·0 (84)	65·6 (96)	18·3 (71)	4·5 (178)
23 April 1955	60·0 (437)	72·2 (220)	†27·1 (410)	8·4 (93)	0 (69)	0 (64)
23 March 1956	36·9 (1195)	43·9 (1282)	8·1 (161)	3·6 (83)	–	–
22 November 1956	1·5 (1033)	1·2 (1692)	–	0·0 (591)	–	
19 December 1956	2·1 (3009)	3·1 (3228)	–	0·2 (441)	–	–
8 January 1957	4·6 (813)	5·5 (943)	–	0·9 (256)	–	–
15 January 1957	4·5 (2113)	5·3 (2253)	–	0·8 (737)	–	–
30 January 1957	9·3 (4274)	7·7 (5268)	–	0·7 (1966)	–	–
19 February 1957	13·7 (3320)	7·5 (6209)	–	0·7 (1787)	–	–
8 March 1957	16·3 (1660)	6·7 (2791)	–	0·7 (1513)	–	–
23 March 1957	19·0 (1605)	8·2 (3449)	–	0·8 (3196)	–	–
5 April 1957	18·0 (1546)	9·2 (1303)	–	1·0 (2889)	–	–
15 April 1957	13·1 (1471)	9·6 (3065)	–	1·2 (2141)	–	–
25 April 1957	15·5 (1221)	9·0 (2602)	–	1·9 (2178)	–	–
4 May 1957	19·1 (680)	5·2 (1190)	–	1·1 (974)	–	–
15 May 1957	–	4·5 (1437)	–	–	–	–

* Samples from 275 m. † Sample from 360 m.

the species was absent from all three samples from above 450 m. A distribution similar to that seen in Swindale and Crowdundle Becks was found from collections made in the upper Spey Valley, Inverness-shire. In the river Feshie at 265 m altitude at its confluence with the Spey at Kincraig, 48% of 462 larvae were

Table 4. Prosimulium hirtipes *larvae in Caernarvonshire streams*, 1952

	Streams	Collecting points	Blackfly larvae	*P. hirtipes*
200-400 m	9	9	226	4
450-800 m	5	15	371	122

P. hirtipes. In another stream at 270 m altitude the proportion in 210 larvae was 16% and in 253 larvae obtained at 400 m in the stream Allt Fhearnagan, 83% were of this species. In this latter stream 82 larvae obtained from 800-1000 m did not include *P. hirtipes*. In contrast with the virtual absence of *P. hirtipes* larvae above about 450 m in the north Pennine and Inverness-shire samples, streams draining

the mountains Carnedd Dafydd, Carnedd Llewelyn and Foel Fras in Caernarvonshire, Wales, yielded a high proportion of the species above 450 m and a low proportion below this altitude (Table 4). It should be emphasized that all samples were obtained between late November and April at sites which on general appearance seemed suitable for *P. hirtipes* larvae. In the north Pennine and Inverness-shire streams there is no obvious change in their character around 450 m, and above this height many apparently suitable sites occur, as suggested by the occurrence of this species up to at least 630 m in Swindale Beck in 1954 (Table 3).

SEASONAL DEVELOPMENT OF LARVAE AT DIFFERENT ALTITUDES

Samples at two to four week intervals were collected from 180 and 300 m stations on Swindale Beck, about 1 km apart. Since the instars cannot be separated with certainty, the larvae were decapitated and the head-widths measured with a microscope fitted with a micrometer eyepiece. Comparison of the size-distributions for the two altitudes (Fig. 1) shows that growth was more rapid at 180 m than at

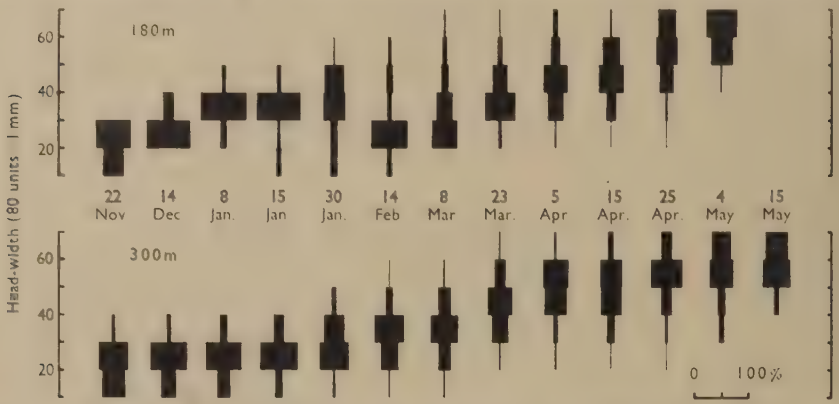

Fig. 1 Size-distributions (percentages) of larval head widths in *Prosimulium hirtipes* from two stations in Swindale Beck, 1956-57.

300 m although differences in the appearance of larvae of the smallest head-width in the two cases complicates the pattern. At 180 m hatching took place in two phases as indicated by the appearance of the smallest larvae. The large 20-30 units head-width-group comprising 60% of the sample on 19 February probably hatched after 30 January but had grown to be included in the 20-30 unit group by 19 February. The indications are that were it not for the occurrence of the large hatch at 180 m in late January and its virtual absence at 300 m, the differences between the two stations later in the season would have been greater. Although hatching may have begun and finished at much the same time, the bulk of the larvae hatched sooner at the higher station than at the lower. Because of this, larvae in the 19 February to 15 April samples were more advanced at 300 m than at 180 m. Differential growth, however, led to those at the lower station overtaking and surpassing those at the higher (compare 25 April with 4 May in Fig. 1). Faster

growth at 180 m than at 300 m is also shown by the differences in the times of appearance and disappearance of the larger head-width groups. Pupation on a large scale had begun at 180 m on 25 April but not until 4 May at 300 m. There is other evidence (p. 341) that limited pupation occurred at both altitudes between 5 and 15 April. Samples taken on three dates in 1956 at 180 and 300 m in Swindale Beck also suggest more rapid growth at the lower station than at the higher (Fig. 2). Larvae at 180 m were more advanced than at 275 m in Crowdundle

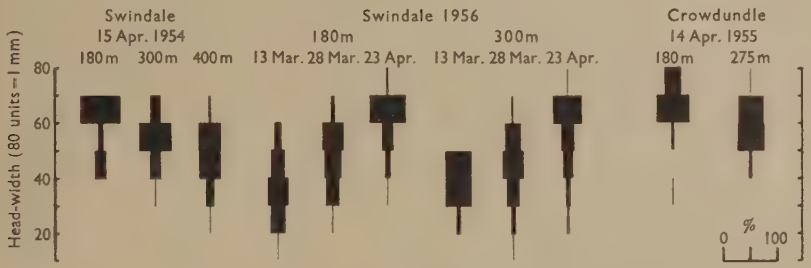

Fig. 2. Size distributions of larval head-widths in *P. hirtipes*.

Beck on 14 April 1955, and a similar picture was given by samples taken on one day at three heights in Swindale Beck in 1954 (Fig. 2).

Correlated with the apparently slower larval growth as the stream is ascended, pupation and emergence were retarded, as is indicated by the proportions on various dates of larvae with black pupal respiratory filament histoblasts (Table 5), an indication of imminent pupation. On 19 May 1955 in Swindale Beck both

Table 5. *Proportion of larvae with black pupal histoblasts, Swindale Beck,* 1957

	180 m		300 m	
	Sample size	% with black histoblasts	Sample size	% with black histoblasts
23 March	305	0	285	0
5 April	279	3·5	121	0
15 April	193	0·5	295	0
25 April	189	7·9	235	0
4 May	130	25·7	62	6·5
15 May	–	–	66	19·7

pupation and emergence had already taken place at 180 m; at 300 m numerous pupae, some empty, were present and no larvae were found; at 400 m larvae vastly outnumbered pupae and no empty pupal skins were found, showing that pupation was at least 2-3 weeks later at 400 m than at 180 m.

Temperature readings in Swindale Beck in 1956-57 using mercury thermometers graduated to 0·1° C held in rapid water and shaded from the sun (Table 6), showed a gradient falling upstream except in early spring. More detailed information was obtained from two mercury-in-steel thermographs whose 6-inch bulbs were placed

in the shade in rapid water on 8 January 1957, one at 150 m and the other at 400 m. Each thermograph was checked against a mercury thermometer at 1-2 week intervals; they gave consistent readings, differing from the thermometer by ±0·3° C. Hourly thermograph readings were corrected to correspond with the single thermometer used for checking both instruments and the thermal sum above 0° C was calculated. Owing to a mechanical defect the clock of the thermograph at 400 m sometimes stopped before the chart was due to be changed. There are therefore short gaps in the record at this height, so that from 8 January to 15 May the 400 m thermograph was in operation for 82% of the time, and that at 150 m for the whole period (104 and 127 days respectively). The thermal sum during the periods when the 400 m thermograph had stopped was estimated on the assumption that the water temperature at 400 m bore the same relationship to that at 180 m as during the previous 7-12 days when both instruments were working.

Table 6. *Temperatures (° C) in Swindale Beck*, 1956-57

	180 m	300 m	340 m
22 November 1956	2·5	2·0	0·9
19 December ,,	5·2	4·7	4·2
8 January 1957	7·8	7·2	6·9
15 January ,,	1·6	0·4	0·1
30 January ,,	4·8	4·1	3·4
19 February ,,	2·1	0·6	0·2
8 March ,,	7·0	6·5	5·5
23 March ,,	8·2	8·7	6·5
5 April ,,	11·8	–	8·5
15 April ,,	8·3	7·4	5·8
25 April ,,	9·2	11·5	7·4
4 May ,,	11·4	13·2	11·0
15 May ,,	9·7	–	9·1

There is no reason to believe that interpolating these estimated thermal sums at 400 m introduced sufficient error to invalidate the conclusions drawn from the results. The cumulative thermal sum in degree-days from 8 January to 15 May for the 150 and 400 m thermographs is shown in Fig. 3. The calculated cumulative thermal sum for 300 m is also shown assuming that temperature conditions at the point were exactly intermediate between those at 150 and 400 m, an assumption which must be approximately true in view of the readings given in Table 6. The water temperature at 400 m was usually 0·2-1·0° C lower than at 150 m, so that the cumulative thermal sum by 15 May was 737 degree-days at 150 m and only 566 degree-days at 400 m; that at 300 m was estimated at 652 degree-days.

The relationship between the thermal sum and the amount of larval growth in a given period was examined by comparing the curves for mean head-width and thermal sums (Fig. 3). In samples taken at 180 m before 19 February the curve of mean head-width was complicated by the discontinuous addition of young larvae newly hatched from eggs, and this part of the curve has been omitted. It is probable that the corresponding curve for 300 m before 8 March was similarly affected so that no measure of growth was possible until after this date. Fig. 1, however, indicates that after 19 February hatching of eggs was probably small enough not to affect the figures appreciably. The upward swing in the larval

growth curve for 300 m and the thermal sum curves which occurred in early March may have been correlated. On the other hand the former might have been caused by the cessation of egg hatching. The failure of mean head-capsule size to increase between 5 and 15 April in both stations possibly reflects limited pupation between these dates, since 'black histoblast' larvae appeared for the first time at 180 m on 5 April (Table 5). The mean head-width curves confirm the size distributions given in Fig. 1, larvae from 180 m being on average smaller than those from 300 m in March and early April, while by 4 May the reverse was true. Fig. 3 shows that there was no close correlation between increase in mean head-

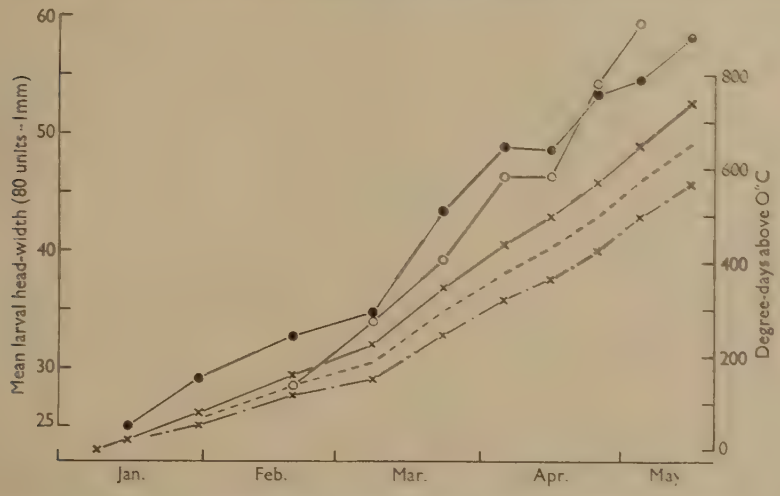

Fig. 3. Mean larval head-width and cumulative thermal sum curves—Swindale Beck, 1957. Head widths: ●——● at 300 m, o——o at 180 m. Thermal sums: x——x at 150 m, x—·—x at 400 m, — — — at 300 m (interpolated).

capsule width and the cumulative thermal sum. This perhaps is to be expected, since we are dealing with an arthropod where an increased speed of development caused by higher temperature between two sampling dates might not lead to moulting until after the second sampling.

SUMMER TEMPERATURE CONDITIONS IN NORTH PENNINE STREAMS

The development of *P. hirtipes* larvae appeared to be completed just before relatively high stream temperatures occurred with the advent of spring, and evidence is given later (p. 342) that they are rapidly killed by water temperatures of 16-18° C. Presumably even a temperature of 15° C would retard development even if it did not prove fatal. It is of interest, therefore, to examine whether streams in the district warmed to 15° C or above in the period from May to September when *P. hirtipes* larvae are absent. Summer thermograph records are available for two streams east of the Pennine ridge in addition to various mercury thermometer

readings. Table 7 shows that even at 600 m in the stream Moss Burn, a small stream, and in Trout Beck, a larger stream 3-6 m in width, temperatures of 15° C and above occurred during the summer months. In the three streams *P. hirtipes* larvae are known to occur in Cross Gill only. All are in or near the Moor House Nature Reserve, and as in most streams east of the Pennine ridge the average gradients are gentle, being of the order of 1 in 15-30 owing to the plateau nature of the country, part of the 'Alston Block'. It may be argued that such streams would be expected to warm up more readily in summer than would the much steeper Crowdundle and Swindale Becks which include stretches at 1 in 5 gradient.

Table 7. *Summer stream temperatures*

Mercury thermometer

	Altitude (m)		Readings	Readings exceeding 14·9 ° C
Moss Burn	605	14 May-23 September 1952	75	21
Cross Gill	300	22 June-11 July 1955	19	16
Cross Gill	300	4-18 July 1956	14	2
Trout Beck	600	9-15 July 1955	5	5

Thermograph records

	Altitude (m)		Days with complete record	Days when water maximum exceeded 14·9° C
Cross Gill	380	28 June-5 September 1951	90	38
Moss Burn	605	15 May-30 September 1953	155	30

Thermograph records for the latter stream for 15 May-5 June 1957 show, however, that water temperatures in excess of 15° C occurred on the following days where maximum temperatures are given: 150 m 1 June, 15·8°; 2 June, 15·0 ; 3 June, 16·4°. 400 m—28 May, 15·0°; 31 May, 15·3°; 1 June, 15·8°; 3 June, 16·8°. On some days the maximum water temperature was higher at 400 m than at 150 m. This effect occurred on sunny days, since at 400 m the stream is in a treeless region and unshaded. For 3 km from 280 to 180 m the stream flows mainly in a shallow tree-lined gorge where by mid-May most of the trees were in leaf, so that shaded conditions probably led to cooling of the water in the lower reaches. This effect may be sufficiently well marked for the thermal sum at 400 m in summer to equal or exceed that at 150 m, so that the converse, found between January and mid-May 1957, may be a winter phenomenon only.

TEMPERATURE EXPERIMENTS ON *P. HIRTIPES* LARVAE

Larvae obtained from 300 m in Swindale Beck were kept in 3-litre jars containing pond water aerated by a rapid stream of air bubbles travelling up a completely immersed tube 2 cm in diameter. The apparatus was essentially similar to that described by Smart (1934). After jars with larvae were set up they were left at 4-5° C overnight and any dead larvae killed during collection or transport to the

laboratory were removed by pipette the following morning. Further mortality was low during the following 2-8 days in control jars kept throughout at 4-5° C. Experimental jars were transferred from the 4-5° C room and subjected to various temperature treatments outlined below. Transfer of a jar from the cold room involved cutting off the compressed air supply for 10-15 sec. Immediately after such a transfer the air supply was interrupted in the appropriate control jar for a similar period. In jars exposed to higher temperatures (16-22·5° C) the water reached the desired temperature within 4-5 h, temperatures being measured by a mercury thermometer every hour during the day time. Dead larvae were removed and counted each morning. The control jars and those kept at 21-22·5° C were

Table 8. *Mortality among* P. hirtipes *larvae at steady high temperatures*

Temp. °C	Cumulative % mortality after number of days shown					Number of larvae
	1	2	3	4	5	
Experiment 1						
4-5° (control)	0·5	4·8	9·2	–	10·8	184
4-5° (control)	6·6	11·9	15·0	–	15·4	228
16-18°	15·0	18·5	50·0	–	97·0	199
16-18°	7·8	16·1	53·1	–	98·1	192
21-22·5°	26·5	82·5	100·0	–	–	98
21-22·5°	39·0	88·5	100·0	–	–	182
Experiment 2						
4-5° (control)	1·4	1·9	2·4	3·8	5·2	218
16-18°, Jar 1	3·9	31·3	81·0	99·4	–	179
16-18°, Jar 2	6·9	37·3	80·8	98·4	–	261

exposed to artificial light during the day only, and those kept at 16-18° C exposed to the natural diurnal light cycle. Since larvae in the field would be exposed to the latter light regime while the controls received only artificial light and suffered very little mortality, the different light conditions cannot have been of great importance as a mortality factor in the experiments. Table 8 shows that larvae at steady temperatures of 16-18° C suffered 50% mortality in 2-3 days while those at 21-22·5° C suffered the same mortality in 1-2 days.

In addition to the 100-200 *P. hirtipes* in each jar there were 1500-2000 larvae of mixed *Simulium monticola* Fried. and *S. variegatum* Meig. To test whether the high mortality in the experimental jars was partly caused by poisoning of larvae by their own waste products, the water in jar 2 (Expt. 2) was replaced after 1·5 days by slowly running 5 jar-volumes of clean aerated pond water at the correct temperature into the top of the jar while water was syphoned off at the same rate from the bottom where larval faecal material accumulated. Table 8 shows that the mortality rate in this jar was comparable with jar 1 where the water was not changed. It is concluded that poisoning was of minor importance as a mortality factor in these experiments and that larvae died mainly as a result of the high temperatures.

Larvae are most unlikely to be exposed in the field to the temperature × time exposures used in the above experiments. Of more practical interest are the effects

of fluctuating temperatures. Here the experimental jars were kept at 4-5° C except for periods of 6-8 h each day when they were transferred to a 23° C room. In this way larvae were exposed to a daily temperature fluctuation five times (days 1-5) of 4·5-18°, 4·5-19°, 4·5-20°, 4·5-20·5° and 4·5-19·9°, respectively. For the following three days (days 6-8) the larvae were kept at 4-5° C. During the 8-day experiment the temperature records show that the larvae were exposed to a total of 24·75 h above 15° C in five periods of 3, 3·25, 6, 6·25 and 6·25 h. On day 3 in jar 2 only, the water was changed as described previously. The mortality on each day (Table 9) scarcely exceeded that in the control after four fluctuations but rose after the fifth, while during days 6-8 when larvae were at 4-5° C considerable delayed mortality occurred. The final percentage mortality suggests that the harmful effect of high temperature was cumulative.

Table 9. *Mortalities recorded among* P. hirtipes *larvae after fluctuating temperatures*

Figures show the % mortality on each day; for details see text.

	Day number							Total mortality (%)	Number of larvae
	1	2	3	4	5	6 7	8		
Control 4-5° C	0·5	0·9	1·8	0·0	0·0	0·0	0·0	3.2	219
Fluctuating temperatures Jar 1	1·9	1·0	0·5	4·9	17·6	36·0	10·3	64·2	204
Fluctuating temperatures Jar 2	2·8	1·9	0·0	3·3	20·4	31·7	7·1	67·2	211

THE DISTRIBUTION OF *PROSIMULIUM INFLATUM* LARVAE

Many collections of larvae and pupae from Crowdundle and Swindale Becks during 1953-57 showed that *P. inflatum* was confined to the extreme headwaters above 660 m altitude. All *Prosimulium* larvae taken below this altitude proved be to *P. hirtipes*, except for a single *P. inflatum* at 630 m on 22 November 1956. Colonization of the streams below the 660 m contour by the latter species must be for some reason impossible. Eggs or larvae must occasionally be washed downstream but presumably such specimens fail to establish themselves in sufficient numbers to appear in samples. Collections from other streams in the north Pennines, the Lake District and the Scottish Highlands have confirmed that *P. inflatum* aquatic stages are found in the headwaters, and localities are listed in a previous paper (Davies 1957). Examination of the headwaters of five streams in Caernarvonshire failed to disclose any *P. inflatum*, and instead *P. hirtipes* larvae were present (p. 338).

ANNUAL CYCLES OF *P. HIRTIPES* AND *P. INFLATUM*

The annual cycle of *P. hirtipes* has already been outlined. During the four years' observations on Swindale and Crowdundle Becks pupation at 180 m occurred in each season during April or early May and emergence of adults from mid-April to mid-May. Records of pupae in other streams and the label dates of museum specimens reared from pupae in various collections show that this is the normal

time in Britain for *P. hirtipes* to emerge, and there is little variation from year to year. Gravid females have been found between 29 May and 10 June. Since small larvae do not appear in streams until the autumn, the eggs of *P. hirtipes* must remain, presumably in diapause, from June-July until October-January, a period of 4-6 months, possibly in gravel in the stream bed as in *Simulium arcticum* Mall. (Fredeen, Rempel & Arnason 1951).

Collections from 1953-55 show that pupation and emergence of *Prosimulium inflatum* occurred in each season from mid-July to mid-August. Pupae were obtained from Crowdundle and Swindale Becks as follows: 1953, 16 July; 1954, 5 August; 1955, 31 July, 30 July to 2 August in the Cairngorms. The predominant size of larvae collected at various dates from March to July was consistent with their achieving full growth between mid-July and mid-August each year. Small *P. inflatum* larvae appeared in the headwaters in the early autumn, and the size of larvae collected in November 1955 and 1956 suggested that hatching probably took place during September and October. Since adults did not emerge until late July or August, the hatching of eggs in September and October suggests that they do not enter a diapause or dormant phase since, allowing 2-4 weeks for the period between emergence and egg-laying by the female, the egg stage must last about 1 month, a reasonable incubation period bearing in mind the probably cool conditions in headwater streams. The larval period is considerably longer in *P. inflatum* than in *P. hirtipes*, lasting from approximately October to July, about 8 months as compared with 4-5 months in *P. hirtipes*. The slower development of *P. inflatum* larvae is illustrated by the fact that larvae obtained in March were of much the same size as those of *P. hirtipes* collected on the same dates, although the latter pupated 1-1½ months later while the former did not pupate for a further 4 months, even though full-grown larvae of the two species are of generally similar dimensions.

There is inconclusive evidence that in abnormally cool years some *P. inflatum* larvae may take two seasons to complete development. A few half-grown larvae have been found in November. It is unlikely that these could have hatched from eggs of the same year for they would have shown an abnormally rapid growth-rate. Furthermore in Allt Fhearnagan, Inverness-shire, larvae collected in late April 1957 showed a well-marked division into two size-groups, which possibly corresponded with specimens hatched from eggs in the autumn of 1955 and 1956 respectively. The middle part of the summer of 1956 was cooler than normal and this may have some bearing on this observation.

DISCUSSION

In *P. inflatum* the long larval life of at least 8 months shows that conditions above 660 m prevent more rapid development, probably directly or indirectly through the low water temperatures there. It is likely but not proven that the larvae are sensitive to relatively high temperatures as has been shown for *P. hirtipes*. Summer temperature readings from the headwater streams are not

available but on general grounds it is thought unlikely that temperatures above 15° C would occur frequently, since a considerable proportion of the water in them is derived from springs and subsoil seepage. The absence of a long egg stage in *P. inflatum* is presumably a feature enabling it to complete its life cycle in a year under conditions where larval life is necessarily prolonged.

The annual cycle of *P. hirtipes* breeding mainly in the lower parts of the north Pennine streams seems to be designed so that larvae occur in streams only when temperatures are low from October to May. The long egg stage from June to October in this species is presumably a method of surviving the summer period of unfavourably high stream temperatures. Since water temperatures above 15° C are likely to occur after about mid-May even at 400 m, *P. hirtipes* larvae should be full grown by this time if they are to avoid exposure to such conditions.

Evidence has been given that in two streams in 1954-57 growth of *P. hirtipes* was more rapid at 180 m than at 300 m. It is possible that the different size-distributions of larvae at the two altitudes could have been produced by the steady washing of larger larvae downstream and not by differential rates of growth. The size distributions at one station on successive dates are, except when egg hatching or pupation were taking place, consistent with the steady growth of all size-groups and give no indication of considerable loss of larvae. Thus in comparing the size distribution on two successive dates from one station, e.g. 180 m on 8 and 23 March (Fig. 1), decrease in the proportion of larvae in, say, the 10-20 units head-width-group between the two dates was accompanied by equivalent increases in the proportions of 20-30, 30-40 size-groups.

From January to May 1957 the thermal sum at 150 m was substantially greater than at 400 m, and there is no reason to believe that this fall in the thermal sum with increasing height is not a normal state of affairs in these streams, at least in winter. It is suggested that the decreasing thermal sum accounts for the apparent slower growth of larvae with increasing altitude. This may act directly on the larvae and partly through its effect on their food organisms. If larval development in winter is retarded as the stream is ascended, a point will be reached above which growth cannot be completed before mid-May. The 8-month larval period in the closely related *P. inflatum* above 680 m supports this idea. It is tentatively suggested that the fact that *P. hirtipes* larvae did not normally occur in numbers above about 450 m in Crowdundle and Swindale Becks is related to the decreasing thermal sum with altitude. It is not suggested that there is a direct causal relation between the thermal sum at different altitudes and the upper limit of *P. hirtipes* larval distribution, since it may well be that the altitudinal distribution of larvae is basically determined by the spatial distribution of egg laying. Presumably in northern England *P. hirtipes* females have been selected so that their oviposition is confined to those parts of the streams usually below 450 m, where conditions are on average suitable for larvae to complete development by the correct time in spring. The work of Ide (1935), Harker (1952, 1953) and Macan (1957) has shown the importance of the direct and indirect effects of temperature on the growth and hence on the annual cycles and distribution of may-fly larvae

many species of which appear to be sensitive to high temperatures as is *P. hirtipes*.

In 1956-57 in Swindale Beck most hatching occurred sooner at 300 m than at 180 m. so that for a period in late winter larvae from 300 m were on average larger than those from 180 m. Insufficient information was obtained to decide whether hatching normally occurs sooner at higher altitudes than at lower. If this is the case it would tend to compensate for the slower growth of larvae with increasing altitude.

The presence of *P. hirtipes* at 450-800 m in the headwaters of each of five streams facing east, north and south in Caernarvonshire in 1952 seems anomalous. If normal, the distribution found suggests that the winter temperature conditions in the Welsh streams at 450-800 m are comparable with those below 450 m in the north Pennine streams. A higher winter thermal sum in north Wales than at a comparable altitude in the north Pennines is not improbable, since Manley (1936, 1942) has shown that the climate at 910 m on Great Dun Fell, adjacent to the headwaters of Crowdundle and Swindale Becks, approximates to that of southern Iceland. Manley (1947) has given evidence that the average duration of snow cover in Wales is less than in the north Pennines even though the former area has a heavier total precipitation, and this may reflect warmer average winter stream temperatures in the former area than in the latter.

The ecological distribution of the larvae *P. hirtipes* and *P. inflatum* in the north of England and Scotland forms an interesting comparison with the situation in northern Norway (Davies 1951, 1954) where in the Holandsfjord district the headwaters and a considerable zone below was occupied by *P. ursinum* Edw. only, with *P. hirtipes* confined to the lower reaches. *P. ursinum* thus occupied a zone roughly corresponding to that of *P. inflatum* in Britain.

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SUMMARY

1. In two north Pennine streams larvae of *Prosimulium hirtipes* normally occurred only below 450 m and those of *P. inflatum* above 660 m altitude.

2. In one stream the thermal sum from January to May 1957 at 400 m was smaller than at 150 m; this is probably normally the case in winter. *P. hirtipes* larvae grow more slowly at 300 m than at 180 m probably, in part at least, because it is colder there.

3. In laboratory experiments temperatures of 18-20° C were harmful to *P. hirtipes* larvae even for short successive daily periods.

4. The restriction of *P. hirtipes* larvae below 450 m altitude may be because above a certain point the winter thermal sum is insufficient to allow larval development to be completed by mid-May, after which date stream temperatures up to at least 400 m may rise to harmful levels.

5. *P. inflatum* larvae probably live under constantly cool conditions and complete development in about 8 months, compared with 4-5 months for *P. hirtipes*. The presence of an egg resting-stage in *P. hirtipes* and its absence in *P. inflatum* appears to be correlated with the environmentally imposed difference in the length of larval life in the two species. There was some evidence that *P. inflatum* larvae sometimes took 2 years to complete growth.

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LOCAL DISTRIBUTION AND DISPERSAL PATHS OF BLOWFLIES IN HILL COUNTRY

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(With Plate 2 and 4 Figures in the Text)

Between July and September 1953 a series of carrion-bait trappings of blowflies was carried out on an upland area of sheepwalks, on the Roxburgh-Dumfries border. The objects of the trappings were to study the distribution of blowflies over terrain showing topographic diversity, to map the pattern of dispersal through the local populations of a released group of blowflies, and to test the effect of a steep hill slope as a barrier to their diffusion. The experimental area (Fig. 1),

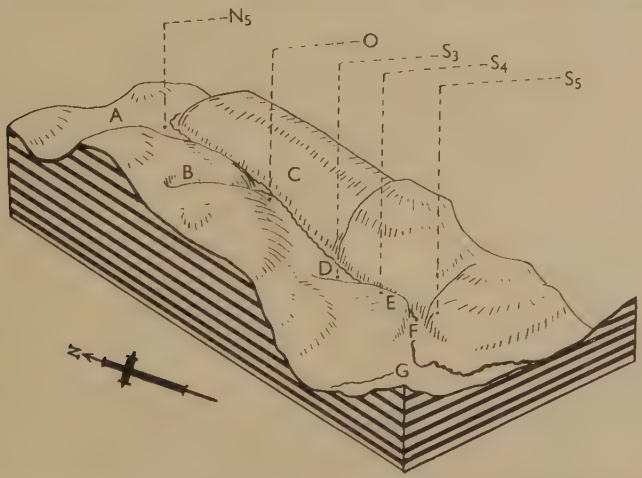


Fig. 1. The Mosspaul valley (not to scale), to show the end basins A and G, the valley proper N_5 to S_4, with the lower defile F, the corrie and gorge B, and the shallow basin D formed by the low spur at E. The east slopes opposite Pylon 0 are shown in Pl. 2*B*.

includes the narrow valley of the Mosspaul Burn, running S.S.W. from the watershed and draining into the Ewes valley, north of Langholm. A main highway runs along the west side of the burn. The upper and lower ends of the valley widen abruptly into broad basins, sheltered by almost complete rings of hills. The upper basin is at an elevation of 800-900 ft; from this the valley drops gently over $1\frac{1}{3}$ miles to about 650 ft, then becoming a narrower, more precipitous-sided gorge, 'the lower defile', which debouches after $\frac{1}{3}$ mile into the lower basin at 600 ft. The sides of the valley proper rise fairly smoothly from the narrow floor to the

crests, at about 1300-1600 ft. The slope of the eastern, *i.e.* west-looking, face is regular and unusually steep, the inclination being mainly 40° to 50°; the western face varies more, with an irregular convex profile at the northern end and a rather concave slope of some 25° to 45° in the lower valley. Midway along the west face a tributary burn descends by a narrow declivity, the 'gorge', at right angles to the valley. Its source is a shallow corrie recessed into the shoulder of the western slope.

PHYSIOGRAPHY AND VEGETATION

Along the floor of the valley is a line of power pylons at approximately 200 yd intervals. We have used these as reference points, numbered from Pylon 0 at the mouth of the gorge as N_1 - - - N_5 and S_1 - - - S_5 to the upper and lower basins respectively. The valley is imagined to be divided by transecting lines through these pylons.

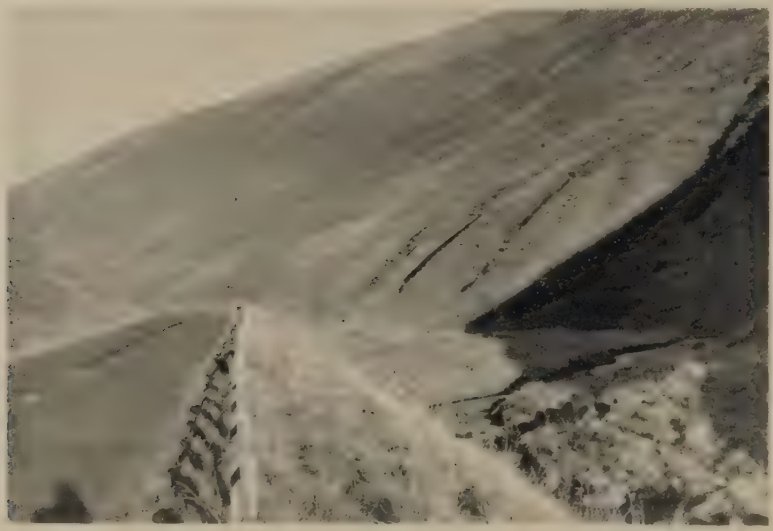
(*a*) *The valley*

The valley vegetation up to about 1000 ft is mainly *Agrostis-Festuca* associated with some *Nardus* and *Deschampsia caespitosa* (L.), while *Carex sylvatica* Huds. occurs in the damper areas. The soil is generally very shallow. The western face is drier than the eastern, and is more deeply scored by dry run-off gullies. On the east face there is limited flushing in some of the shallow gullies. Above 1000-1100 ft the vegetation on both sides is a dense growth of *Molinia;* the west side above 1500 ft is capped by a *Calluna-Sphagnum* bog on deep peat. On the west side, south of the gorge, bracken occurs below the *Molinia* belt as dense stands with intervening diffuse growth. There is a downward encroachment over the Pylon interval S_3-N_1, reaching to within 100 ft of the roadway between Pylons S_1 and 0. The bracken extends up the north side of the gorge, and reappears again in the N_4-N_5 interval. Over the east face it occurs as a more diffuse growth with some small discrete stands. The floor and lower slopes are mainly bracken-free except for occasional solid stands beside the burn.

The bed of the burn, some 4-10 ft wide, is to some extent sheltered by the roadway, which has also affected the secondary drainage so that the vegetation of the valley floor differs from that of the lower slopes, being characterized by *Juncus* and more frequent *Molinia* tussocks.

At the lower end of the valley the sides close in, the western slope at Pylon S_4 projecting south-eastwards to form a low, almost flat-topped spur (Fig. 1, E) which partially blocks the exit of the valley except for the lower defile. This latter begins in the S_3-S_4 interval as an eroded channel which rapidly deepens as the spur closes in and curves round the base of the spur, undercutting it, to debouch into the south basin near the Pylon S_5 level (Fig. 1, F). The south-eastern aspect of the spur, the 'western' face of the defile, is an almost vertical drop of some 50 ft to the roadway, about 20 ft above the watercourse. Along the floor of the defile is a considerable thicket of alder. The steep western bank and the crest above are covered with dense bracken, with bramble and willowherb; the bracken extends

A. Looking down on the lower defile and the south basin from the east slopes opposite Pylon S_4. Pylon S_5, not seen in the picture, is almost in line with the stone wall on the left. In the right foreground is the low spur at Pylon S_4 and centrally the steep western side of the lower defile.



B. The eastern slopes, looking north-east from near Pylon S_1. The gorge is beyond the spur on the left. The L_{1E} trap-line was about the level of the two sheep at the head of the pair of short dry-gullies; L_{2E} was in the *Molinietum* showing white near the summit.

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over the flat top and into the S_3-S_4 interval. The west face here is recurved by the spur to form a shallow shelter basin (Fig. 1, D), so that the lower slopes of the S_3-S_4 interval have a more directly east aspect than the rest of the western face. The east face, over this interval, forms a particularly steep-sided and rounded buttress which shelters but also shadows the valley floor.

Northwards from Pylon 0 the western slope alters, rising almost vertically for the first 50 ft or so, then curving away more gently from this false crest, which is covered by a crisp growth of bent-fescue with blaeberry. North of N_3 the valley gradually widens; the floor is alluvial and almost flat and under the influence of a tributary burn on the west of the road, has a mainly damp rank vegetation. In the N_5 subsection the sharp initial rise of the west face has largely disappeared, and with the decreasing height of the slope the vegetation approximates more to the rank valley-floor type.

(*b*) *The end basins*

The south basin (Fig. 1, G and Pl. 2*A*) is formed by an irregular widening of the head of the Ewes valley. The sides are covered by a continuous belt of *Molinia*; in the cultivated floor are farm buildings, arable fields, hay pastures and bent-fescue grazings, with considerable bracken, mainly as dense stands. A straggling growth of alder lines the watercourse. The north basin, a high *Molinia* moor, is a similar cultivated floor, ringed by lower and rather less steep hills, pierced on the east and west by watercourses and with the northern watershed forming a col over which the highway passes to drop into Teviotdale (Fig. 1, A). The vegetation of the central area, apart from the hayed fields, is mainly bent-fescue, with *Molinia* on the slope, and a moister complex, with *Carex* spp. and *Juncus* spp., in the recessed watercourses. Immediately north of the valley is a farm-type set of buildings, with a few trees.

(*c*) *The corrie and gorge*

The high corrie lies in the *Molinietum* on the western face, its floor being at 1200 to 1300 ft (Fig. 1, B). At the back of the basin there is almost perpendicular scree-face, with interrupted bracken-heather association, the sides, mainly *Molinia*-covered, curving round with increasingly gentle slope to the corrie lip. The gorge which descends from the corrie floor is densely clothed on its northern face with bracken, which extends northwards on to the main slope, and upwards on to the floor of the corrie, which it penetrates for some distance. On the damp shallow soil of the south wall of the gorge there occurs a narrow strip of *Eriophoretum* which has extended on to the well-drained floor of the corrie.

NARRATIVE OF THE EXPERIMENT

The trapping was done in three phases.

Phase 1. From 23 July to 1 August a preliminary series of five trappings was made of the floor and lower slopes of the valley between Pylons S_3 and N_3. On each occasion 125 traps were used, alternate traps being baited with rabbit

and herring. Over 625 trap-days, a total of only 1030 blowflies were caught. These were killed for identification.

Phase 2. From 3 to 14 August flies were caught for marking and release. The catches were pooled in five cages in the laboratory, with sugar and water. The cages were of about 9 cu. ft capacity, and until the final trapping the density was kept under 500 blowflies per cage. From experience of laboratory-reared cage colonies densities of this order do not appear to be excessive, and in fact two samples retained in the laboratory as longevity controls after release of the main groups

Table 1. *Phase 2 trapping. Daily catch of calliphorines for marking*

Traps out	Area	No. of traps	Exposure	Catch	Total to release cages	Nett release
3 August	S_3-N_2	125	4-7 h	29		
			48 h	18		
5 August	S_3-N_3	236	24 h	20		
6 August	S_3-N_4	271	6-8 h	151		
		180	24 h	127		
7 August	,,	224	2-7 h	76		
		177	24 h	60		
				481	450	141
8 August	,,	196	7-10 h	156		
		206	24 h	6		
9 August	,,	271	24 h	93		
				255	126	106
10 August	,,	231	24 h	223		
11 August	S_5-N_3+north and south basins	321	6 h	264		
				487	418	265
11 August	S_5-N_3	271	24 h	302		
12 August	S_5+south basin	?	8 h	136		
				438	341	231
12 August	S_5+south basin	50	8 h	215		
13 August	,, ,, ,,	189	6-8 h	20		
14 August	,, ,, ,,	179	6-9 h	425		
				660	643	415
			Grand Totals	2321	2121	1158

showed normal longevity (50% dead at 3-4 weeks, 95% at 6-8 weeks, according to species).

The sequence of trappings and total catch are given in Table 1. Up to 10 August the traps were distributed as in Phase 1. A total of under 1000 blowflies was caught for about 1400 trap-days, and on 11 August some of the traps were put out in the north basin and some in the lower defile and south basin. The greater part of the catch was from the latter group, and so on the following

and subsequent two days all available traps were concentrated in the south basin and the mouth of the lower defile.

The earlier caught flies were now beginning to show wing fraying from the prolonged confinement, and in view of the lateness of the season and the uncertainty of an improvement of catch level it was decided to start the experiment on 15 August with the material available, although the numbers were undesirably low. The cage colonies of wild flies were given a radioactive label by feeding P^{32} for two days in the drinking water (MacLeod & Donnelly, 1957a). Cage colonies of laboratory-bred *Phormia terrae-novae* and other species were labelled by paint-marking of the individual flies. We are concerned here only with the *P. terrae-novae* material, as only one recovery each was made of the other laboratory-bred species.

The flies were identified, and individually monitored for radioactivity as they were transferred from their cages to the carriers for release; with two exceptions, a *Calliphora* with no count and a *Phormia* with a very low count, all gave a distinct positive reading. Identifications of the *Lucilias* was merely as *L. sericata* or *L. caesar* group, and the latter may have included some *L. silvarum*.

Phase 3. The marked wild flies were released at Pylon 0 at 6 p.m. on 18 August. Between 4 p.m. and 9 p.m. distribution of traps according to a prearranged pattern was completed for the greater part of the area, but a few of the more distant groups of traps were distributed early on 19 August. The *Phorma terra-novae* material was released on 20 August. Recovery trapping was continuous until 9 September, the bait, mixed rabbit and herring per trap, being renewed usually every second day. The trap positions were visited daily, with one or two exceptions, and all traps containing Calliphorines brought in to the laboratory, fresh traps being substituted.

The distribution pattern of the 178 trap-positions used for the Phase 3 trapping was as follows. A line of traps with a frequency of three traps per pylon interval lay along the valley floor between pylon transects S_5 and N_5, with parallel lines rather less than 100 yd away along each valley face. Thus a succession of thirty rows of three traps in line abreast transected the floor and lower slopes of the valley at approximately 70 yd intervals. The trap lines are referred to by their levels, L_0 on the valley floor, L_{1W} and L_{1E} the first level on the west and east slope respectively. The L_{1W} trap line ran through heavy bracken and bramble in the S_5-S_4 interval, through the thinning bracken in S_4-S_3, crisp bent-fescue as far as S_2-S_1, where it entered the lower fringe of the large western bracken mass. From the north face of the gorge it ran along the exposed false crest and entered the bracken again at N_4-N_5. The L_{1E} line traversed an *Agrostis-Festuca-Nardus-Deschampsia* complex, rather more lush than on the west face, for its whole length.

Between pylon transects S_2 and N_2 two further lines of three traps per pylon interval were placed on each face at approximately 1000 ft (L_{2E} and L_{2W}) and 1200 ft (L_{3E} and L_{3W}). The L_{2E} trap line at 950-1000 ft traversed rather similar vegetation to L_{1E}, except that it was mainly in a zone transitional between the bent-fescue and the *Molinia*, and containing some diffuse bracken, occasionally

forming loose patches. The L_{3a} trap line at 1200-1250 ft was in the *Molinia* zone. Physiographically the whole of this eastern upper slopes area was a uniform smooth plane (Fig. 1 C and Pl. 29). On the west face, the L_2 trap-line at 1050-1100 ft penetrated the upper limits of the bracken mass south of the gorge, and on the northern side was under the influence of the shorter and sparser bracken extending outwards from the gorge to the N_1 transect. The L_{3a} trap-line, at 1200-1300 ft was entirely in the *Molinia* zone; its central traps, on each side of the gorge, were on the lip of the corrie.

The floor and slopes of the corrie were sampled by nine traps and a set of four sampled the gorge. Because of the curvature of the valley, causing the transecting rows to diverge opposite the gorge, extra traps were inserted on the east face in the S_1-N_2 interval, two in L_{3a} and one each at L_{3a} and L_4. One trap was placed at Pylon 6, which was half way between the L_{3a} and L_4 trap lines. This was the release point for the marked flies. At each end of the valley twelve traps were distributed over a rough half-circle of about ¼-mile radius extending outwards into the basin.

The trapped area is regarded as consisting of six sections: the valley proper, the south basin section which includes the lower defile (S_1), the north basin, the east and west upper slopes, and as a special section the high corrie and gorge. The valley section is assumed to extend slightly beyond the L_2 trap lines, *i.e.* about 300 yd up each face; it thus consists of a row of more or less equal-sized subsections, each approximately 200 sq. yd. separated by transecting lines at the pylons. They are referred to by the outer limiting pylon number, *e.g.* the subsection from Pylon S_4 to Pylon S_5 is called S_5. The upper slopes sections each consists of two subsections one at each trap-line level: the west slopes section is bisected by the narrow channel of the gorge.

NUMBERS AND SPECIES DISTRIBUTION

(a) *Distribution in relation to topography*

The total catches of native unmarked flies over the Phase 3 period (excluding 19 August) are given in Table 2; the species and their sex-ratios are expressed as catch per trap. Where subsections were trapped in obvious physiographic subdivisions such as the three levels in the valley subsections, the results are grouped accordingly. Since the catches represent the total caught over twenty-one days, it is obvious that the catch per trap on any one day was very low for even the more favourable areas. The low catches make insignificant many of the differences between subsections, and for simplicity the main valley subsections have been grouped for Fig. 2 in five reasonably homogeneous areas: (*a*) S_2—the distinctive lower defile; (*b*) S_4 and S_5—because of the slight basin in the western face here the valley is slightly broader than further up, and the western face is rather less steep, with a lower crest; (*c*) S_7 to N_2—the central block of subsections; (*d*) N_3—the western face at this point is at its steepest, making the valley quite narrow at the L_2 and L_3 level; (*e*) N_4 and N_5—the slopes fall away gradually over this block and the floor of the valley widens.

Table 2. *Phase 3 trapping: total native flies caught*

Figures give the numbers of flies caught per trap (males : females) of each species or group of species. In this and succeeding tables *C.e.* = *Calliphora erythrocephala*, *C.v.* = *C. vomitoria*, *Lc.* gp. = *Lucilia caesar* group, *L.s.* = *L. sericata*, *P.t-n.* = *Phormia terrae-novae*, *Cyn.* = *Cynomyia mortuorum*.

	Traps	Total catch	*C.e.*	*C.v.*	*Lc.* gp. (*L.s.*)	*P.t-n.*	*Cyn.*
South basin	12	1609	16·8:44·5	15·6:25·1	5·2:22·8(0:0·08)	0·4:0·6	1·3:1·7
S_5:L_{1W}	3	554	26·3:47·3	16·3:13·0	15·3:58·7	2·0:2·3	1·7:1·7
L_0	3	948	30·7:76·0	61·0:97·7	8·7:41·0	0·7:0·3	0:0
L_{1E}	3	247	11·7:31·3	11·3:13·7	1·7:5·0	0:0·7	1·7:5·3
S_4:L_{1W}	3	56	3·0:7·3	0·3:0·7	0·7:2·0(0:0.7)	0:0	2·7:1·3
L_0	3	416	12·7:40·0	21·7:37·7	5·0:17·7	0:0·7	0·3:2·3
L_{1E}	3	88	2·7:15·3	2·3:4·7	0:1·3	0:0	1·3:1·7
S_3:L_{1W}	3	63	3·0:9·3	0·7:2·0	0·3:1·3	0:0	2·0:2·3
L_0	3	104	2·0:14·7	6·0:9·3	0:1·0	0:0	0:1·7
L_{1E}	3	81	1·7:17·7	1·0:2·0	0:0·7	0:0·3	0·3:3·3
S_2+S_1:L_{3W}	5	106	1·4:12·2	1·8:1·8	0:0	0·2:0	1·0:2·8
L_{2W}	6	146	2·8:12·7	1·0:2·0	0·2:0·5(0:0·2)	0:0	0·3:4·7
L_{1W}	6	82	0·8:7·2	0·7:1·5	0·2:0·7	0:0	1·0:1·7
L_0	7	146	3·0:8·7	2·4:3·6	0·1:0·6	0:0·1	0·7:1·6
L_{1E}	7	147	2·6:11·7	1·9:2·7	0:0·1	0·1:0	0·6:1·3
L_{2E}	7	173	2·3:15·4	1·1:2·0	0:0·9	0:0	0·7:2·3
L_{3E}	6	120	1·5:13·0	0·2:1·3	0:0·5(0:0·2)	0:0	0·5:2·8
N_1+N_2:L_{3W}	5	139	2·6:12·4	1·2:1·6	0:0·6	0:0	2·6:6·8
L_{2W}	6	160	3·3:16·7	0·7:1·3	0·2:1·0	0:0	1·2:2·5
L_{1W}	6	93	1·8:8·7	0·2:0·7	0:0·3	0·2:0	1·0:2·7
L_0	6	109	2·0:9·8	1·7:3·0	0:0·7	0:0·2	0·3:0·7
L_{1E}	6	182	1·8:18·2	1·5:3·0	0:0·3	0·2:0	2·5:2·8
L_{2E}	7	213	2·6:16·9	1·7:2·4	0·1:0·3	0:0	2·7:3·7
L_{3E}	6	145	1·3:13·0	0·8:2·7	0:0·7	0:0	1·3:4·3
N_3:L_{1W}	3	99	2·7:20·3	2·3:2·7	0:0·3	0:0	2·3:2·3
L_0	3	55	1·7:8·7	3·3:1·3	0·3:0·3	0:0	1·3:1·3
L_{1E}	3	109	2·0:20·3	3·0:5·0	0:0·3(0:0·3)	0:0	2·3:3·0
N_4:L_{1W}	3	129	6·3:23·7	2·0:5·0	0·3:0·7(0:0·3)	0·7:0	0·7:3·3
L_0	3	124	5·0:14·2	7·0:8·7	0·7:3·0	0:0	0·7:2·0
L_{1E}	3	78	2·3:12·3	2·3:2·0	0·3:0·7	0:0	2·3:3·7
N_5:L_{1W}	3	106	5·6:16·7	5·0:3·7	0:1·3	0·7:0·3	0·3:1·7
L_0	3	192	8·0:17·0	15·3:15·3	1·7:4·0	0·3:0·3	0·7:1·3
L_{1E}	3	132	5·7:23·0	3·0:4·0	1·0:0·7	0:0	2·3:4·3
North basin	12	989	15·2:33·2	11·3:16·2	0·8:2·1	0·2:0·4	0·7:2·5
Release point	1	57	15·0:19·0	7·0:2·0	0:2·0	1·0:1·0	5·0:5·0
Gorge	4	199	5·3:16·3	9·8:13·0	0·3:1·3	0:0	1·0:2·5
Corrie floor	3	182	3·3:17·0	13·0:16·3	0·3:1·3	0:0·3	5·7:3·3
Corrie slopes	6	286	6·7:21·2	5·8:8·5	0:0·7	0:0	1·5:3·3

The results for the three trap rows of each of these five blocks and for the two end-basins are illustrated in Fig. 2. The relation of numbers and species distribution to elevation is also shown (Fig. 2*c*), the catches for the trap rows at levels 2 and 3 being compared with those for the central block S_2 to N_2. This overall

picture of the distribution requires a breakdown for time effects before conclusions can be drawn, but the following points may be made at this stage: (1) Between the limits of 750 and 1200 ft elevation had apparently no effect on numbers. The north basin, however, had a distinctly lower density than the south basin, some 200 ft lower. This difference is largely due to the relative scarcity of *Lucilia* spp. in the north basin. (2) There was a remarkable uniformity of species pattern, as

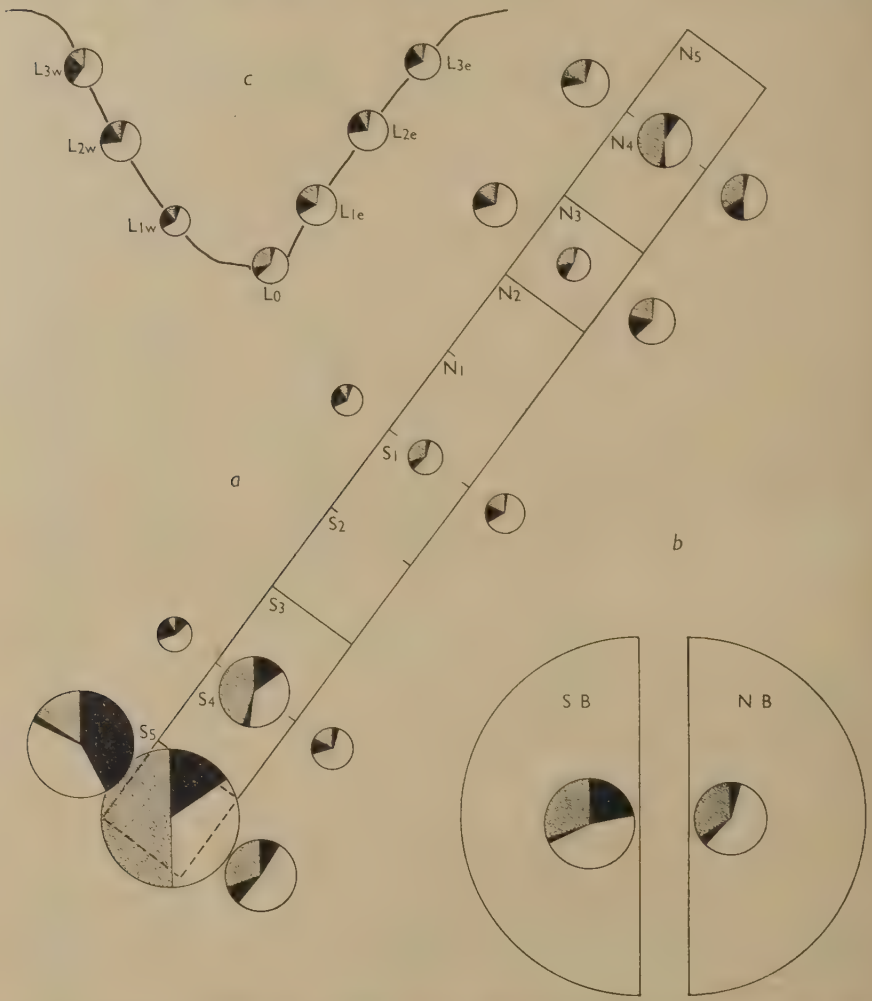

Fig. 2. Relative areas (indicated by the sizes of the diagram divisions) and the catch per trap (areas of circles) for: *a*, the valley subsections; *b*, the end basins; *c*, the pylon intercept S_2-N_2 at elevations of 700, 850, 1000 and 1200 ft. The three circles for each valley division are for the L_{1W}, L_0 and L_{1I} traps. Circle segments, clockwise from noon: *Lucilia* spp. (black), *Calliphora erythrocephala* (white), *Cynomyia* (black), and *Calliphora vomitoria* (stippled); the rarely occurring *Phormia terrae novae* has been included with *Lucilia*.

well as of numbers, at the different elevations. (3) The male : female ratio of *Calliphora erythrocephala* was usually about 1 : 4, but the males tended to be in slightly higher ratio in the end basins and the S_5 subsection, on the western slopes of S_4 and S_3, and on the floor of the valley from S_2 to N_5. The *C. vomitoria* males were usually in a 1 : 2 ratio, and showed little variation except that they were relatively fewer on the high eastern slopes. *Cynomyia mortuorum*, with a ratio of about 1 : 1·5, had relatively more males on the western slopes of S_5, S_4 and S_3; the species showed occasional concentrations of females but no trend in relation to terrain. The *Lucilia caesar* group ratio was about 1 : 4, but the numbers were too low to show any distribution pattern on the sexes. (4) The single trap at the release point had a much higher catch for all species than the comparable L_0 and L_{1W} traps of subsection S_1. It is possible that some of these were actually liberated flies which had lost their paint mark or radioactive label, but this could account at most for only a small part of the discrepancy, and the high total catch for this trap remains unexplained.

(*b*) *Time changes in population level and distribution*

The catches per trap given above for the various subsections are the pooled results for the Phase 3 trapping period; during this period both the totals and species patterns showed considerable variation, much of it represented by erratic day-to-day fluctuation. These fluctuations showed no apparent correlation, for any of the species, with the two-daily change of bait, nor incidentally does bait age appear to be responsible for the erratic variation in sex ratio observed, particularly in the *Calliphora erythrocephala* catches.

To separate major trends from this erratic fluctuation, the daily catches during the Phase 3 trapping may be replaced by running means. All the Phase 1 trappings and the Phase 2 trappings up to 10 August were done in the subsections S_3 to N_4, mainly S_3 to N_3. We have thus a record of the catches for this block of subsections over a time range of seven weeks. In Table 4 (Col. 1), are given the catches per trap for individual trap days in Phases 1 and 2. From these figures and from the total for subsections S_3 to N_2 during the Phase 3 trapping, smoothed as a running mean of three days, the changes in fly density in this central area of the valley over the seven weeks have been graphed (Fig. 3*a*). The figure shows that the density was consistently low, and showed no overall trend.

The time-changes in the different parts of the valley (over the Phase 3 period only) are compared, on the basis of catch per trap per day, in Fig. 3*b*, *c*. The curves for subsections S_3 to N_4 were very similar, differing only in elevation, and to make the figure more easily interpreted the total range for the group is shown as a shaded band. The figure shows that whereas the main part of the valley, from S_3 to N_4 had little variation in its low fly density until the last week when it rose to over twice the earlier level, the end subsections of the valley proper, N_5 and S_4, had a population peak during 23-27 August, and the end basins, particularly the south basin, a still more pronounced peak at this time. In both pairs the peak was followed by a trough, the curves in the final week corresponding to those of

the central valley subsections. The lower defile subsection, on the other hand, with the highest initial density, maintains this difference throughout; except for the three days 28-30 August and the last two days the curve-level is almost double that of the other subsections. In contradistinction to the horizontal comparison, the comparison of different elevations (Fig. 3*c*) shows negligible difference between the three elevation levels in the shape of the time-density curves.

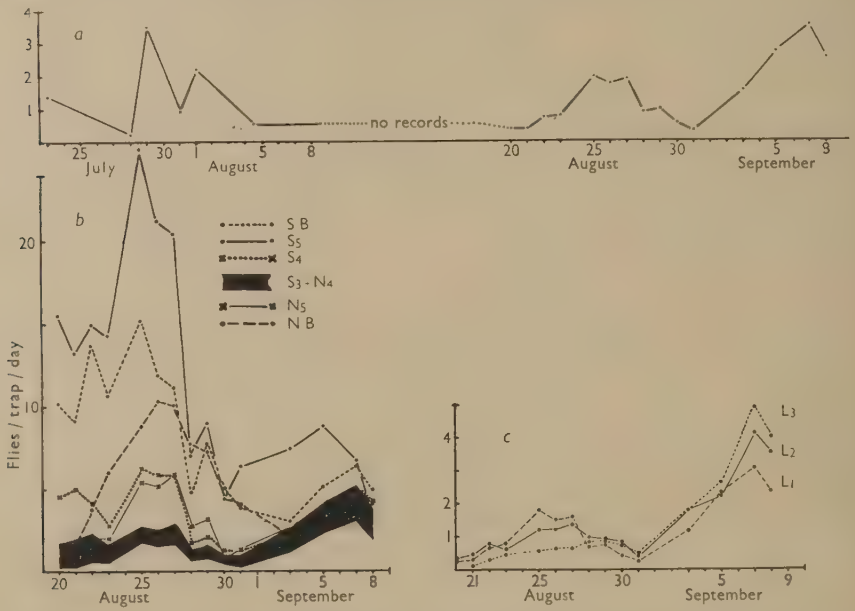

Fig. 3. *a*, Population level (3-day running mean) over seven weeks in the valley S_3-N_3.
b, Time curves of population level (3-day running means) for horizontal subdivisions. The broad band indicates the limits of range of the group of curves for subsections S_3-N_4.
c, Time curves for the upper slopes 3_W+3_E, the intermediate slopes, and the valley floor and lower slopes $L_0+L_{1W}+L_{1E}$, over the same horizontal interval S_2-N_2.

It is to be noted that in the horizontal series of subsections the day-to-day ranking is consistent, *i.e.* the population groupings, at subsection level at least, were apparently not ephemeral. In the elevation series, although the day-to-day ranking of the levels remains consistent, there is apparently a complete reversal of ranking order between 23-27 August and the final week.

(*c*) *Time changes in species pattern*

During the Phase 3 period appreciable changes occurred both in the relative overall density of the different species, as judged by the trap catches, and in their individual distribution patterns. Thus *Calliphora erythrocephala*, the overall numbers of which were apparently greater at the end of the experiment, had increased mainly in the northern part of the valley, and on the slopes. The *Lucilia caesar* group largely disappeared after 27 August, but before this a distinct

change occurred in its regional distribution. The statistical significance of the regional groupings, and the change in pattern, for these two are examined in Table 3. The variance estimates of the differences between areas have been derived by the method previously described (MacLeod & Donnelly 1956); for the standard deviation formulae, the pooled subsections S_4+S_3 and S_2-N_2 and the corrie are regarded as of subsection level of uniformity, the remaining areas as sections. The divisions of the area are listed in the first column of the table. The gorge, with only four traps and consequently a high error of mean catch, has been omitted. The *Calliphora erythrocephala* mean catches for 26 August are given in the next column. Those for the two subsections of the south basin section do not differ significantly, and are pooled as a section mean. N_3 has been combined with N_4+N_5, with section variance. The slopes have also been pooled. The resulting seven areas are compared for significance of catch differences (upper left of table). The catches for the same areas on 5 September are given in the final column, and are compared in the lower right of the table. Obviously significant differences or absence of significance are merely indicated (+ or N.S.); the error of the difference is given where the significance is marginal.

On 26 August the slopes catch was significantly lower than the others (Col. 1 of differences); the south basin section (top row, across from 10·4), was significantly higher, except for the north basin. By 5 September, the slopes (bottom right-hand row) differed significantly only from the south basin, which further differed only from the corrie and central block (read down last column of differences). The catch for the northern subsections of the valley on the other hand had gained a significant lead over that for the central block.

The catches for the *Lucilia caesar* group are similarly examined for 21 August and 26 August. With this group also the south basin subsections and the slopes sections have been treated as single areas; the low catches in the north end of the valley and the north basin have been combined as a section mean. Reading across from means 7·2 and 1·7 we see that the south basin and S_4+S_3 were significantly different from each other and from the other four areas; by 26 August, however, while the south basin catch remained significantly higher than the others, that of S_4+S_3 was no longer so. The effect is due to the decrease in the lower valley and south basin catches, and to an absolute increase in the central and to an even greater extent in the northern valley populations.

The nature of the changes in population level of the different species can be more clearly examined by comparison of the species pattern for the two peak periods shown in Fig. 3*b*. In Fig. 4 the catch per trap for the two *Calliphora* species for the four catch days 22-26 August is represented by the lower half-circles, that for the four catch days 5-9 September by the upper half-circles. The traps were not visited on 24 August or 6 September. For the figure the subsections have been grouped into: the central area, S_3 to N_4 of the main valley section, the two extreme subsections S_4 and N_5, the lower defile, the two end-basins, the slopes and the special section (including the single release-point trap situated near the entrance to the gorge).

Table 3. *Significance of differences between areas*

Calliphora erythrocephala

Area	Mean catch 26 August		Differences 26 August: Slopes	Corrie	N.B.	N_3-N_5	S_2-N_2	S_4-S_3	South basin	Mean catch 5 September	Area
S.B.	8	10·4	+	7·3 ± 2·75	N.S.	+	+	7·3 ± 2·62		7·95	South basin
S_5	13·67										
S_4 + S_3		3·06	2·48 ± 0·85	N.S.	N.S.	N.S.	N.S.		N.S.	3·83	S_4+S_3
S_2-N_2		1·66	1·08 ± 0·44	N.S.	3·34 ± 1·77	N.S.		N.S.	5·7 ± 2·01	2·27	S_2-N_2
N_3	1·1	1·74	1·16 ± 0·58	N.S.	N.S.		2·43 ± 1·19	N.S.	N.S.	4·7	N_3-N_5
N_4+N_5	2·06										
N.B.		5·0	4·42 ± 1·75	N.S.		N.S.	N.S.	N.S.	N.S.	3·83	N.B.
Corrie		3·1	2·52 ± 1·18		N.S.	2·9 ± 1·36	N.S.	N.S.	6·15 ± 2·12	1·8	Corrie
W. slopes	0·5	0·58		N.S.	N.S.	N.S.	N.S.	N.S.	5 ± 2.04	2·96	Slopes
E. slopes	0·65									2·96	Slopes

Differences 5 September

Lucilia caesar group

Area	Mean catch 21 August		Differences 21 August: Slopes	Corrie	N_3-N.B.	S_2-N_2	S_4 + S_3	South basin	Mean catch 26 August	Area
S.B.	6·9	7·2	-	-	-	-	5·5 + 1·97		3·67	South basin
S_5	7·7									
S_4 – S_3		1·7	1·64 ± 0·58	1·59 ± 0·66	1·34 ± 0·6	1·65 ± 0·58		2·95 ± 1·09	0·72	S_4 - S_3
S_2-N_2		0·05	N.S.	N.S.	N.S.		N.S.	-	0·18	S_2-N_2
N_3	0	0·36	N.S.	N.S.		N.S.	N.S.	+	0·46	N_3-N.B.
N_4+N_5	0·33									
N.B.	0·42									
Corrie		0·11	N.S.		N.S.	N.S.	N.S.	+	0·11	Corrie
W. slopes	0·05	0·06		N.S.	N.S.	N.S.	N.S.	+	0·10	Slopes
E. slopes	0·08									

Differences 26 August

The numbers of *C. erythrocephala* females show little change in the end basins and lower defile, whilst the valley, the upper slopes, and the gorge and corrie, where the density was relatively low, all show pronounced increase. The increase on the slopes was more marked on the upper than the middle slopes. The males have decreased in the basins, the lower defile, and the gorge and corrie. It is of interest that these areas provide the most shelter, either from physiography or from rough vegetation. In the less broken-surfaced valley subsections their density has remained unaltered, whilst on the exposed slopes their numbers, though low, show ninefold increase. The population of *C. vomitoria*, on the other hand, shows a marked decrease generally. The female populations have levelled

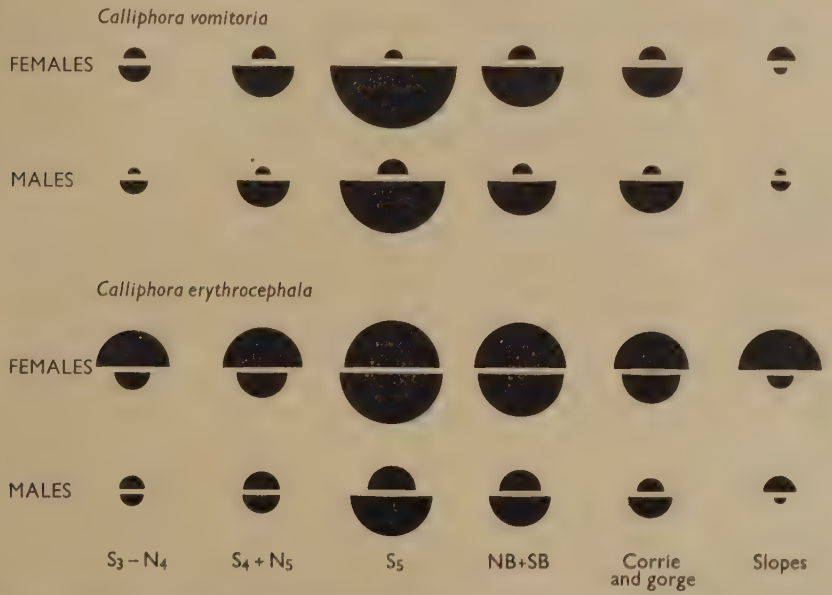

Fig. 4. Local populations of *Calliphora vomitoria* and *C. erythrocephala* by sexes: lower half circles, 22-26 August; upper half-circles, 5-9 September.

out to a fairly uniform low density (0·6 to 1·2 per trap) irrespective of their earlier density; *e.g.* the lower defile, initially 24, and the central part of the valley, 1·5, have both decreased to 0·6. On the exposed slopes the initially low densities of populations have actually increased to bring them within this late density range. The males have decreased, but to levels proportional to the initial numbers rather than to a common level.

The *Lucilia caesar* group had also decreased markedly, and except on the slopes the males had practically disappeared. The low numbers of *Phormia terrae-novae* caught showed no consistent difference between the two trapping periods. The *Cynomyia* population had roughly trebled its numbers in all subsections except on the slopes, where the increase was even more pronounced.

It is clear from Fig. 4 that the marked decrease in the total catch after 27 August, shown in Fig. 3*b* for the lower, more sheltered part of the valley (S_4 and S_5), for the end basins, and for N_5, was due mainly to the decrease of *Calliphora vomitoria*. The corresponding decrease in *Lucilia* spp., which were concentrated mainly in the lower defile and south basin, accentuates the change in the curves of total numbers for these two areas. It is also evident that the reversal of ranking order of the different elevations (Fig. 3*c*) is due to the greater relative increase of *Calliphora erythrocephala* on the slopes than in the floor of the central valley, and to a less extent to the similar changes in relative distribution of *C. vomitoria* and *Cynomyia mortuorum*.

The species proportions in the valley area S_3 to N_3 for the above two periods are compared in Table 4 with those obtained during the Phases 1 and 2 trappings

Table 4. *Time-changes in species proportions*

Date	Total catch per trap-day	Percentage of total catch				
		C.e.	*C.v.*	*Lc.* gp.	*P.t-n.*	*Cyn.*
S_3-N_3						
23 July	1·4	77	14	1·2	–	7·5
28 July	0·23					
29 July	3·5	69	21	2·5	1·2	6·2
31 July	0·92	76	11	–	4·0	7·8
1 August	2·2	74	12	3·6	5·0	6·1
3- 7 August	0·56	62	15	11	5·8	5·8
8- 9 August	0·54	75	2·8	10	8·8	2 8
22-26 August		43	40	6·25	0·9	8·9
5- 9 September		77	7·0	0·7	0·6	14·7
S_5. Zero level						
13-14 August		44	19	36	1·0	0·6
22-26 August		26	62	11·5	0·4	–
5- 9 September		66	29	5·5	–	–

of the same area. The Phase 2 species proportions are those for the pooled catches in the first two cages. The species proportions in the catch of 11 August over this area are not known as the catch was pooled with other catches before identification. The proportions for the L_0 traps in the lower defile may also be compared with those for the Phase 2 trapping on 13-14 August, which was concentrated in the valley bottom where later the L_0 trap-line ran. The table indicates the rise and fall of the *Lucilia* population, in July and September, and an early August peak for *Phormia terrae-novae*. In this part of the valley, of only marginal suitability for *Calliphora vomitoria*, the fluctuations are such as to obscure the significance of the final low relative catch, particularly as the simultaneous catch in the favourable S_5 floor area is still above the mid-August level.

(*d*) *Summary of species distribution*

The highest densities of the *Lucilia caesar* group were in the S_5 subsection, the south basin, and subsection S_4 in that order. In the S_5 subsection the catch in the L_{1W} traps was much higher than that of the L_0 traps. The L_{1W} traps were on the

flat crest of the cutting, among dense bracken or bramble, and sheltered on the north by a stone wall lying a few yards back from the crest. In S_4 the highest catch was in the L_0 traps. In this subsection the valley floor was not such a deep channel as in S_5, and the L_{1W} traps, though dominated as in S_5 by bracken, were in less luxuriant growth and were on a more exposed brow, with a longer diurnal exposure to sunshine. Over the remainder of the valley the density was low, but slight concentrations were found in the L_0 traps of N_4 and N_5. On this broadening alluvial flat were rushes and other rank growth but no bracken, although there was a diffuse interrupted growth on the lower face of the adjacent eastern slope. The north basin, gorge and corrie floor, and S_3 had more or less similar and low densities, and also the S_2-N_2 transect, where the catches remained uniformly low irrespective of height. It is to be noted that these uniformly low densities occurred on low ground relatively sheltered but bare (the L_{1W} trap-line of S_3), at intermediate elevation sheltered but with only occasional cover (the north basin) or with rank cover in almost permanent shade (the gorge), and at high elevations sheltered and with partial rank cover (the high corrie). Since the air temperature in the north basin was presumably distinctly lower than in the south basin, these results suggest that the *L. caesar* group require for optimum physiographic conditions air warmth and topographic shelter, but these must include respectively exposure to insolation and the cover of rank vegetation.

Of the four *L. sericata* trapped in the valley section, three were on the lower west slopes, and one on the east slopes. None were caught in the valley floor.

The distribution of *Calliphora vomitoria* differed from that of the *Lucilia caesar* group in the following respects. The proportion concentrated in the south basin and S_5 was less, viz. the ratio of the *L. caesar* group to *Calliphora vomitoria* in this section is 2:3, that in the S_4 subsection 2:5, while elsewhere it varied from 1:5 to 1:10, the disparity being least on the slopes and greatest for the corrie floor and gorge. As with the *Lucilia caesar* group, elevation over the S_2-N_2 transect had apparently no effect on numbers. In S_5 the L_{1W} trap-line did not appear to be nearly as favourable as the L_0 traps, which had three-fourths of the total catches in S_5, and the highest catch also in S_4 and S_3. The corrie floor and gorge, the north basin and the L_0 traps of N_5 had relatively high catches. The presence of this species in numbers in the L_0 traps of N_5 and to a less extent of N_4 is of interest, since these traps were not in bracken or other tall growth. This is in disagreement with the findings in the Crosby experiments that the species was virtually confined to formation types with high-field-layer.

The distribution of *Calliphora erythrocephala* shows a surprisingly close agreement with that of *C. vomitoria*, if compared over the period preceding 30 August, when a rapid decline in numbers of the latter set in. *C. erythrocephala* occurred rather more on the slopes, and rather less in the corrie and gorge section. The species were about equal in the end basins and in the valley except for the extreme subsections S_4 and N_5, where *C. erythrocephala* was fewer. It was distinctly fewer in the lower defile.

Phormia terrae-novae formed a small concentration at the low west spur of S_5,

otherwise only isolated captures were made. With two exceptions, one on the corrie floor and one on the west slopes, these were all along the valley section and in the north basin, *i.e.* it appeared to be restricted to shelter rather than vegetational cover.

Cynomyia mortuorum showed a fairly steady increase in density both northwards along the valley and up the slopes; in the latter the numbers per trap more than trebled between L_0 and L_3 on both aspects. The highest density was on the corrie floor and the lip of the corrie to the north side (L_{3W} over N_1 and N_2). In the valley section the higher catches were mainly in the L_{1E} traps from N_1 to N_5. No specimens were taken in the floor of the lower defile, while ten and twenty-one respectively were caught in the west and east L_1 traps. If the temperature in the floor of the defile is assumed to have been lower than that on the rim at L_{1W}, then it would appear that exposure, as much as cool temperatures, is a controlling requirement for concentrations of this species.

CLIMATE AND WEATHER RELATIONS

Maximum and minimum temperatures were read daily from Six's thermometers at 5 ft at Pylons S_3, 0 and N_3. Only slight and irregular differences were obtained between the temperatures at these three points in the valley floor. The daily maximum during the Phase 3 period varied between 15·5° and 20° C, except for 6-9 September when it lay between 21° and 24° C. The minimum ranged between 7° and 11·5° C, with a low exception (3·3° C) on 29 August. On 10 September, simultaneous readings of temperature and humidity were taken by whirling hygrometers for th efive trap-line levels, L_{2W}, L_{1W}, L_0, L_{1E} and L_{2E}. A series of readings, one at each trap point, and synchronized by the operator at L_0, were taken along the levels by five men moving abreast from N_2 to S_2 and back to N_2. The readings were all between 11·40 a.m. and 1 p.m. B.S.T., and during this time none of the observers was in shadow from the ground contour. The results were unexpected; the west slopes facing E.S.E. had a higher air temperature, and the east slopes a lower, than the valley floor. To the north of the gorge, where the western profile is convex the side becoming less steep between L_{1W} and L_{2E}, the upper level was warmer than the lower on the first run, the advantage disappearing by noon; southwards from the gorge, the concave-profiled slope had a higher temperature on the lower than the upper slopes. The humidity on both east and west slopes was slightly higher than in the valley bottom. The observations were repeated a week later, series of readings being taken in the forenoon, early afternoon, and evening. In the forenoon, the highest temperatures were recorded on L_{1W}, the lowest on L_{2E}; L_{1E} was slightly warmer, and L_{2W} slightly colder, than the valley floor. By the afternoon the slight temperature advantage of L_{1E} had disappeared, the levels ranking as on the previous week, $L_{1W} \simeq L_{2W} > L_0 > L_1 > L_{2E}$. In the evening L_{1W} was still the warmest, L_{2W} being now appreciably cooler, but still no colder than the lower eastern slope L_{1E}.

The western slopes facing E.S.E. receive the greatest morning insolation and the upper part of the convex face north of the corrie, being almost normal to the

incident rays, will get the maximum. Since the valley is obstructed at S_4 and subsequently opens at an angle into the Ewes valley, air drainage is slowed down and the cold air flowing down from the slopes overnight will tend to fill the valley bottom. The normal reduction of temperature with height may thus be balanced for much of the day by the trapped cold air in the valley bottom, and the effect would be accentuated on the western slope by morning insolation. This may have happened to the extent that on the above occasions the recognized nocturnal inversion of temperature in valleys of this type persisted through the day. Whatever its origin, this curious inversion, or at least disappearance, of the temperature gradient of the ground-air zone may well have been present for much of the recovery period, and could account for the absence of an inverse correlation of numbers with height (Fig. 2*c*). It leaves two unexplained difficulties, however. There is negligible difference between the catches on the sun-warmed western slope and on the eastern slope receiving only sky radiation and assumed to have a lower temperature than that of the valley floor. Secondly the piling up of cold air in the valley floor should affect the lower defile, where the highest population levels were found, to a greater extent even than the mid-sections S_2-N_2.

Meteorological readings were taken daily at Pylon 0 during the Phase 3 trapping. In addition to the Six's thermometer, instruments included a thermo-hygrograph, solar radiation thermometer (black bulb *in vacuo*), rain gauge, Piché evaporimeter and aneroid barometer. The Daily Weather Report (Meteorological Office) records of wind speed and direction and of sunshine hours for Eskdalemuir Observatory, about eight miles west on the same hill range and at a similar altitude (778 ft), have been used as representative of the Mosspaul area. The observatory records for rainfall, which are given separately for day time and night, have also been used as a check on our own single daily records.

No clear association was obtained between any one weather element and the changes in numbers of the different species trapped, nor could the relative changes in distribution between the different areas be related to the daily weather, as recorded at Pylon 0. The general weather pattern during the experiment, as given in the Daily Weather Report, may be summarized for the Border country as follows: in late July the weather was dominated by a series of large depressions, giving a south-westerly to westerly type, rather cool and wet. Early August had mainly anti-cyclonic weather in the locality, but by the end of the second week this deteriorated and for the last fortnight a pronounced westerly type persisted, with frequent rain, except for a short spell of fair weather about 25-26 August, relapsing on 27 August to a south-westerly type with rain. This lasted until 5 September when anti-cyclonic conditions brought fair weather with three really fine days, 6-8 September. On 7 September the anti-cyclonic type gave way to a north-westerly type, cooler, but still fine and dry. The above picture is only indifferently well reflected in the meteorological records for the valley, and it is clear, in retrospect, that the Pylon 0 site was quite unsuitable, as indeed would any single station have been, for illustrating the particular weather of this topographically unusual area.

An abrupt decline of the *Lucilia* population occurred on 27 August. This was common to all the areas where the species had previously been trapped. There was no pronounced change of any measured element to correspond with this decline, and their numbers in the traps subsequently remained negligibly low on days with higher air and sun temperatures and less wind and rain than some of the days of high catch preceding 27 August. Similarly, a decline of *Calliphora vomitoria* numbers except on the slope occurred on 31 August, and their numbers remained low subsequently, even during the period 6-8 September with warm air temperature, long sunshine hours, and high insolation. Although the catches of *C. erythrocephala*, except in the south basin section, were higher during the warm weather period 6-8 September than in August, there is again an absence of direct correlation of the catches of individual days with their weather elements. Even if the *C. erythrocephala* population of the central valley floor only, S_2-N_2, is compared with the Pylon 0 records, little improvement in their agreement is obtained.

There is some association of total numbers with the synoptic weather picture, *vide* the peaks during the anti-cyclonic periods 25-26 August and 6-8 September. This supports the recent suggestion of Wellington (1957) that the impact of meteorological conditions on insects could probably be studied more profitably by relating micro-climatic conditions to atmospheric movements rather than to static macro-climatology. The synoptic weather picture, however, does not in itself account for the changes in the *C. erythrocephala* population, the females of which at least were apparently not undergoing weather-independent decline similar to that of the *C. vomitoria* and *Lucilia* populations. There is of course the possibility that eco-climatic changes conditioned by frontal zones of air-masses were in fact governing closely the variations in trapped numbers, but we have no information from which to examine this.

INDIVIDUAL DISPERSAL IN RELATION TO POPULATION GROUPINGS

(*a*) *Dispersal paths of released flies*

Of the wild-caught flies given a radioactive label, the numbers of viable flies released on 18 August and the numbers recovered between 19 August and 27 August were: *Calliphora* spp. 853 (106), *Lucilia* group 236 (27), *Phormia terrae-novae* 54 (2), *Cynomyia* 15 (4). In addition, a nett total of 147 laboratory-bred and paint-marked *Phormia terrae-novae* were released on 20 August. Of these, 18 were subsequently recovered. No radioactive or paint-marked flies were recovered after 27 August.

The releases were made at Pylon 0 in the evening. One labelled *Calliphora erythrocephala* female was caught in the south basin about a mile away in the afternoon of the following day. Others were recovered from the corrie slopes, at nearly 1500 ft, and from the north basin, on 21 August. Similarly labelled *C. vomitoria* were recovered from the floor of the high corrie on 20 August and from the south basin on 21 August, *Lucilia caesar* in the north basin and on both east and west mid-slopes, and a paint-marked *Phormia terrae-novae* on the east upper

slopes on 21 August. Thus all the species except *Cynomyia* dispersed within three days to the limits of the trapped area. The marked *Phormia* specimen taken at the L_{3E} level, the only recovery in this trap-line, was in a trap on the Pylon 0 transect, so that this one-day flight, if a direct one, represents a sheer climb and not a long traverse. Five of the *Cynomyia* releases were recovered, four of them in the neighbourhood of the release point; the fifth was on L_{2W}. The single laboratory-bred *Lucilia sericata* recovered was taken in the north basin about $\frac{3}{4}$ mile from the release point on the second day after release.

There is no evidence from the results that the steep slopes of the valley exercised any deterrent effect on dispersal of *Calliphora erythrocephala* or *Phormia* which were recovered near the summits, or of the *Lucilia caesar* group several of whom were recovered on the mid-slopes.

(*b*) *The pattern of dispersal*

The relationship of density of released flies to the density of the native populations is shown in Table 5 for the main subdivisions of the terrain. When a large number of marked flies are released at one point, it is to be expected that an immediate effect will be a high rate of catch in the nearer traps, encountered while the released flies are still concentrated. This rate will decrease with distance, as the concentration decreases through dispersal. The distribution of the recoveries on 19 August is therefore tabulated separately for *Calliphora erythrocephala*, *C. vomitoria* and the *Lucilia caesar* group, the recoveries for 20 August to 27 August being pooled to give a measure of the dispersal pattern after the initial concentration had largely dissipated. Of the laboratory-bred *Phormia terrae-novae* material released on 20 August, four were recovered on the following day, one at the release point, one in the gorge, one in N_2, on the L_{1E} level, and the fourth in the highest trap line on the east face, L_{3E}.

It is evident from Table 1 that more than half of the surviving wild-caught flies released on 18 August were originally trapped between 12 August and 14 August in the lower defile. There is no evidence from the laboratory-maintained control samples that the flies were debilitated by the period of confinement, and it is unlikely that this short history of conditioning to the laboratory climate would have induced an atypical reaction to the valley climate, manifesting itself in the direction of dispersal of the released flies. It is nevertheless clear from Table 5 that the dispersal pattern, at least in so far as it is measured by the distribution of recoveries, does not resemble the pattern of population groupings of the local flies over the same period. The *Calliphora erythrocephala* recoveries on the first day show as expected a peak near the centre of the valley tailing off outwards, though the tail is more prolonged down valley; the other two species similarly show a central concentration of recoveries. In all three the central peak is displaced slightly down valley, *i.e.* is in S_1+S_2, and not equally divided between S_1+S_2 and N_1+N_2. This drift was in the face of a moderate south-west to south wind for 19 August. After the first day, however, this faint similarity of recovery to population groupings disappears. The *C. erythrocephala* recoveries apart from a (probably residual)

central peak are more or less indifferently distributed up and down the valley and over the open slopes. *C. vomitoria* has apparently dispersed mainly by the narrow gorge and to a less extent down valley; none were recovered, even among moderate local concentrations, northwards along the valley floor to the north basin. The *Lucilia caesar* group releases apparently spread uniformly in all directions; the numbers of recoveries per area all lie between one and four, except for one nil result, although the corresponding native samples vary widely. The *Phormia* results, though more suspect in that the recoveries were not of native origin, are particularly interesting. With the exception of two in the special section, the native flies caught were all from the valley floor and basins. Of the eighteen marked flies, six were in the neighbourhood of the release point, six from the open slopes, three from the gorge and corrie, and only three from the basins. None was caught along the valley floor.

Table 5. *Distribution of recoveries in relation to native population groupings*

Figures in parentheses show the numbers of marked flies trapped.

	19 August			20-27 August			
Section	*C.e.*	*C.v.*	*Lc.* gp.	*C.e.*	*C.v*	*Lc.* gp.	*P.t-n.*
North basin	7 (0)	3 (0)	4 (0)	221 (4)	222 (0)	24 (3)	4 (2)
Valley							
N_5 to N_3	8 (2)	3 (0)	4 (0)	153 (2)	178 (0)	35 (2)	4 (0)
N_2+N_1	3 (1)	1 (0)	0 (1)	51 (2)	32 (0)	5 (2)	1 (1)
S_1+S_2	6 (29)	2 (3)	2 (4)	61 (14)	56 (2)	9 (1)	2 (2)
S_3+S_4	4 (4)	7 (1)	9 (0)	124 (6)	194 (2)	79 (1)	1 (0)
South basin							
S_5	20 (1)	39 (2)	94 (0)	321 (2)	466 (1)	268 (4)	5 (0)
South basin	22 (1)	42 (0)	78 (0)	363 (4)	344 (1)	222 (0)	3 (1)
Release point, gorge and corrie floor	(No trapping)			67 (3)*	143 (8)	13 (4)	2 (8)
Corrie slopes, and upper levels—west	(Areas incompletely trapped)			151 (5)	82 (1)	9 (2)	0 (3)
Upper levels—east				48 (3)	33 (0)	9 (4)	0 (2)

* All at release point, along with 10 unmarked.

All but eight of the recoveries were taken by 23 August. Since during the four days 20-23 August, except for the morning of 22 August, the wind was consistently between S.S.W. and W.N.W., the directions taken by the recovered flies were apparently independent of wind direction.

(*c*) *Significance of differences in native and recovery patterns*

The distribution of the native flies (Table 5) is assumed to be dependent on the terrain subdivisions; the distribution of the dispersing marked flies forms in all the species an apparently different pattern from that of the natives. Whether this difference is significant may be examined by testing the recoveries : natives ratio for independence of the terrain classes. If there is no significant interaction the ratio may well be an attribute of the marked population (in this case the proportion they formed of the total population) and the observed discrepancies merely

sampling error. A significant interaction on the other hand will indicate that the ratio is probably contingent on the density level of the natives. If that be so, the dispersal pattern itself must be independent of those terrain factors which decide the pattern of native density.

The results as tabulated were used for *Calliphora erythrocephala* and *C. vomitoria*; for the *Lucilia caesar* group the N_2+N_1 and S_1+S_2 results were pooled to give adequate numbers for χ^2 test. The summed χ^2 values are, respectively, >80, >40 and >80. With 9, 9, and 8 degrees of freedom these are significant well beyond the 99% probability level. On the assumption of independence, the pooled χ^2 will obviously be nil (since the expected ratio is the observed ratio), so the summed χ^2 represents only interaction χ^2. The difference in the patterns of the marked and native flies may therefore be confidently regarded as real. The low numbers of *Phormia terrae-novae* preclude χ^2 test, but if the recoveries in each area are regarded as occurrences in samples from a binomial distribution, the 95% confidence interval for the 11% of marked flies trapped in the south basin section (0-50%), and that for the 80% trapped in the special section (44-97%) only overlap slightly.

DISCUSSION

In an earlier paper (MacLeod & Donnelly 1957b), an attempt was made to relate the observed groupings of populations of blowflies to the structural characters of the vegetation cover. It was shown that, although an ill-defined association existed, the relation of numbers of any one species and vegetational habitat-structure was not constant, and differences in population level occurred which were apparently unrelated to structure. In the present paper the possibility of interaction of topography and vegetation in determining population distribution is examined. Differences in elevation of up to 500 ft, without gross associated differences in structure, have in this instance produced negligible evidence of effect either on the total numbers or the species pattern of local populations. The result is complicated, however, by the probability that in this particular valley there was during the observations some degree of inversion of temperature gradient.

Routine meteorological recordings of the standard macroclimatic type were made at one station arbitrarily positioned in the area. Examination of the results was unprofitable, and this aspect of the work has been only cursorily discussed. It could well have been omitted, were it not that it is a salutary confirmation of Wellington's stricture (1957) on this type of bioclimatic observation: 'It is impossible to use the most precise and detailed weather records with biological data collected with no special thought for the weather or its possible effects.'

The degree of topographically conditioned shelter, as might be expected, affected the population density of all the species examined; the quality and the extent of the association differed between the species. Since, however, the vegetation pattern is usually related to the topography, the sheltered areas possessing the most of the woodland formation and high-field-layer field formation types, local concentrations

of high density, or local scarcity, of a species could seldom be attributed simply to the topographic characteristics of the locality. It should be pointed out also that where very low catches are involved, as in the greater part of the area except for the south basin section, comparison of densities on the basis of catch per trap may be misleading, as $2n$ traps will not necessarily catch twice as many flies as would n traps. Where the number of traps is as great or greater than the density of a particular species within the zone of influence of the group of traps, it is obviously correct to base comparisons on the catch per area, but unfortunately there is no information in this study from which we can estimate the proportionate extent to which available flies were trapped each day.

Bearing in mind the above, we may generalize from the observed distribution of species in relation to terrain. *Lucilia sericata* finds open ground exposed to the sun more favourable than ground more sheltered from the wind but more shaded, but there is the probability that in this case the sheltered and shaded valley floor was at least occasionally cooler than the western lower slope. The *L. caesar* group favour conditions which provide high-field-layer, but only where this is associated with topographic exposure to sunshine. Local concentrations may occur in absence of high-field-layer (*e.g.* the floor of S_4, N_4 and N_5), where there is good shelter from wind without continuous shade. *Phormia terrae-novae* prefers topographic shelter from wind irrespective of temperature, but apparently not vegetational shelter. *Cynomyia mortuorum* tends to occur on exposed aspects and apparently finds topographic shelter unfavourable, not necessarily directly since there was a concentration in the high corrie, but possibly because topographic shelter is usually associated with high-field-layer or wood formation. *Calliphora erythrocephala* appears to be tolerant of a wide range of conditions, but the maximum concentrations are apparently more associated with vegetational than topographic cover, and good exposure to sunshine appears to be unimportant. It may occur in moderately high concentrations however on exposed ground which has little vegetational cover. *C. vomitoria* is more restricted than is *C. erythrocephala* to high-field-cover, but moderate concentrations may occur in topographic shelter without rank growth (*e.g.* the high corrie and the floor of N_4-N_5) to a greater extent than the earlier observations at Crosby indicated.

In this relatively high and cool area, an apparent seasonal decline of the *Lucilia* group and of *Calliphora vomitoria* started during the observation period. The drop in trapped numbers occurred in both cases on days of poor overall catch associated with poor weather conditions, but the catches did not in either case recover with return of apparently suitable weather. The decline would therefore appear to be an effect of the earlier history of these populations and not an accident of seasonal deterioration of the weather. Associated with this decline there is in the *Lucilia caesar* group results an apparent shift of population from sheltered to more open habitats, the central and northern end of the valley and the slopes showing absolute increase in catch although the overall catch had declined. There is a similar suggestion in the *Calliphora vomitoria* results, in that the slopes show absolute increase in density of females. The catches were so meagre, however,

that the totals for the two periods illustrated in Fig. 4, if regarded as samples from a Poisson distribution, might well belong to the same statistical population.

Although the numbers of *C. erythrocephala* females increased towards the end of the period, there was a marked drop in the numbers of males. It is known that males decrease in numbers before the females at the end of the season, and the *C. erythrocephala* population may also have been in imminent decline. If this were so, it is interesting that the males should first begin to disappear in the apparently most favourable areas. If their relative increase on the open slopes is also due to seasonal shift as suggested for the *Lucilia caesar* group and for *Calliphora vomitoria*, is this simply due to accelerated dispersal of high foci, because of a seasonal disappearance of the centres of attraction within arenas previously rich in such sources of population grouping, or does it represent a time lag, in the less favourable habitats, in emergence of the last generation of the season?

Perhaps the most important information obtained from this experiment is that supplied by the recoveries of marked flies. These were made during the first period of high catches, when the species studied except *Cynomyia* were present in some density in their chosen habitats. The distribution pattern during the first few days after release of a concentration may be regarded as representing the actual process of dispersal. It is unfortunate that no recoveries were made after the first week, for the pattern after say two weeks might have given interesting information on the extent to which the survivors of these released individuals had been marshalled into groups, and the extent to which such grouping could be related to the physical environment. It is clear that the dispersal movements of the different species were not directed to the areas of optimum conditions, as indicated by the density pattern of the native populations. It has been suggested (Williams *et al.* 1956) that for two at least of the blowflies, *Calliphora erythrocephala* and *C. vomitoria*, there is in Europe a definite southward migration in autumn. Setting aside in the meantime the possibility of a seasonal migration impulse, one would not expect the nomadic individual to be aware of the existence, let alone of the relative suitability, of lands beyond its horizon, nor would one expect this horizon, the limits of its sensory perception, to be at all extensive. Oriented reactions, however, or even klino-kineses, to micro-gradients of temperature, pressure, air movement or reflectance from the ground below them, might reasonably have been expected to influence the direction of the dispersal paths of the individuals of each species, in relation to ground masses and planes, or their cover, so that they would tend to be shepherded towards the areas favourable for the species. There is no evidence of such orientation of flight, except that the shelter-loving *C. vomitoria* was recovered from the sheltered gorge and floor of the high corrie but not from the open. Failure to recover it from the open slopes, however, might be due as suggested by Wardle (1927) less to its absence than to a lessened ability to detect carrion in the open.

If we accept then that dispersal originates as aimless outward flight from the release point, any significant channelling of dispersal should be due to simple avoidance deflection of the undirected flight of individuals which happen to cross

the boundary between a favourable and a less favourable area. One *Lucilia caesar* at least was not checked from adventuring beyond the bracken cover into the *Molinietum* slopes above the high corrie. On the other hand, none of the recoveries had penetrated beyond the highly favourable lower defile to the rather less favourable south basin. This, however, might be an ortho-kinesis effect. Among the *Phormia terrae-novae*, the avoidance deflection should have tended to keep the releases milling around in the valley floor, an effect which was conspicuously absent.

Finally, any suggestion of grouping would be expected to be due to slowing-up kineses becoming operative as the dispersing individuals blundered across favourable habitats. It is interesting in this connection that the four *Lucilia caesar* group flies caught in the east upper slopes section were all in the bracken-influenced L_{2E} subsection, whereas one of the two *Phormia terrae-novae*, which is not a high-field-layer species, was taken in the *Molinia* subsection beyond this (L_{3E}). Similarly, *Calliphora erythrocephala*, which apparently favours high field cover although not confined to it, was not recovered beyond the bracken line on the upper slopes section; but two were recovered from the slopes of the high corrie.

From the foregoing, and bearing in mind the fact that recoveries were made at different limits of the experimental area within a day or two of release of the flies, it would appear that the immediate reaction to release of a concentration of flies is that the individuals disperse aimlessly in all directions. This flight is in many cases rapid and sustained, so that some flies are a mile or more away from the point of release within a day. The dissipation of the concentration is apparently not canalized to any great extent by the nature of the terrain, but the rate of spread of the flies may be slowed down locally by encounter with favourable arenas.

It is possible that the initial flight reaction is a result of the period of cage-confinement, and that the compulsion to travel fast and far, suggested by the pattern of the early recoveries, is not a normal behaviour pattern. It seems reasonable to assume, however, that after their first burst of flight the individuals react as do the native flies to the environmental stimuli of the moment. In such case it follows that the normal individual is not territorially restricted, its nomadic movements are undirected and may equally well bring it over favourable or unfavourable arenas. Presumably, an aimless flight may at any moment be interrupted by the attraction of some 'centre of action' and the fly be drawn to, and dally with, the source of the sensory stimulus, to take wing again after satiety, the direction perhaps a mere accident of orientation when taking off, and the airborne fly merely expressing the urge of the individual towards continued movement. In unfavourable habitat the flight will be mainly fast and random, the interruptions mainly compelled by exhaustion of available carbohydrate; in favourable habitat there may be orthokinetic slowing-up of flight, and the frequency of interruption will be to a large extent related to the concentration and diversity of sources of sensory stimulus. At any moment of time, therefore, the population might be expected to show a pattern of more or less marked groupings, associated with the biotic or physiographic mosaic, but this aggregation would be

an extrinsic effect on the population, and not due to a gregarious tendency of the individuals.

This interpretation calls for an examination of the concept of an isolated population. We are apt to accept, unconsciously, the implication that the limits of an isolated habitat are like a boundary wall preventing outward spread of the inhabitants. With a nomadic fly population, this will not be true; the boundary of the area will not halt dispersal, for the same reason that the edge of a flat disc does not halt the outward spread of a central heap of dry sand. The isolated area is isolated only from immigration, to an extent determined by the distance from other population centres. An island in the seas will suffer continuous dissipation of its population over the shore-line, since none of the random flights which cross the border can be followed by a reversed-direction flight from accident of orientation at the next take-off. An island surrounded by terrain unfavourable for maintenance of a population of its own will differ only in the rapidity of the loss, since a proportion of the outward flights, which will normally be considerably less than half, will by random chance effect a re-entry.

SUMMARY

1. The distribution of Calliphorine blowflies over the floor and slopes of a narrow valley in the Southern Uplands of Scotland was studied by intensive trapping over a period of three weeks in August and September.

2. Preliminary trapping over the previous three weeks showed that the total blowfly population in the area was consistently low. The *Lucilia caesar* complex and the *Calliphora vomitoria* populations declined during the observations, apparently seasonally. *C. erythrocephala* increased slightly, but a decrease in males suggests the imminence of seasonal decline of the population. *Cynomyia mortuorum* increased markedly.

3. Associated with the seasonal decrease of the *Lucilia caesar* group there was a distinct redistribution with relatively greater concentration in open terrain. A similar population shift to more exposed habitats is suggested in the results for the two *Calliphora* species.

4. The population levels in different subdivisions of the area were significantly distinct in many cases. An attempt is made to relate the density of the different species to the physical and vegetational characters of the subdivisions. Over the central subdivision of the valley, where there was no pronounced difference in structure-type of the vegetation or in physiography only slight differences were found in the total catches and species patterns at elevations ranging from 850 to 1300 ft.

5. Laboratory-bred *Phormia terrae-novae* and locally trapped *Lucilia caesar* group and *Calliphora* species were marked and released in the valley. Specimens were recovered within one or two days at the confines of the trapped area up to 1 mile from the point of release. There was no evidence of canalization of dispersal by ground contour. All these species were apparently able to disperse up

an incline of approximately 45° extending to a vertical height of 500 ft above the release point.

6. The direction of individual dispersal was apparently random for these species, and the distribution pattern of recovered flies over the ensuing week was not related to the corresponding pattern of the native population groupings.

7. It is suggested that the direction of individual flights is normally random, that these flights are interrupted with varying frequency according to the concentration of attraction sources, and that their speed as well as duration varies in different fly-arenas. Population groupings thus develop in favourable habitats, where the activity arenas contain more minor centres of action, and where slowing-up kineses are more likely to be induced by eco-climatic or other physical conditions. Habitat selection is therefore by the population, and not by the individual, and the resulting density mosaic persists despite the tendency of individuals to random dispersal.

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PREDATION BY TITS AND SQUIRRELS ON THE EUCOSMID *ERNARMONIA CONICOLANA* (HEYL.)

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(With Plate 3 and 6 Figures in the Text)

The observations described in this paper form part of an investigation into the relationship between insectivorous birds, chiefly tits (*Parus* spp.), and their food in the State Forest of Thetford Chase, East Anglia, from 1952 to 1957; other results are appearing separately (Gibb 1957, Betts 1958). Thetford Chase consists almost entirely of plantations of scots pine (*Pinus sylvestris*) and Corsican pine (*P. nigra*), planted from about 1922 onwards; the former predominate. Thetford Chase has been described by Macdonald (1939) and the ecology of the district by Watt (1936).

Quantitative measurements of the predation by insectivorous birds on their prey are always difficult and often impossible to make in the field. Most of those so far attempted have been made in the birds' breeding season, when insect food is particularly abundant and when individuals of many species of prey are vulnerable for a comparatively short period. Consequently it has generally been found that at that season insectivorous birds eat only a small proportion of their prey (references in Lack 1954, ch. 13). Even so, Tinbergen (in press) calculated that predation by birds on caterpillars in summer could contribute significantly towards the stability in the numbers of certain Lepidoptera in Dutch pine forests. In winter, however, individuals of many species of insects are vulnerable to predation by birds for several months. The larvae of *Ernarmonia* (*Laspeyresia*) *conicolana* (Heyl.) (Lepidoptera: Eucosmidae), which spend the winter in pine cones, are a notable example.

Blue tits (*Parus caeruleus*) and to a lesser extent coal tits (*P. ater*) are the chief predators on *conicolana* larvae; and in winters when the larvae are common they are an important food. The tits' feeding behaviour will be described from observations in the field and on captive birds in an aviary (Gibb 1957). Red squirrels (*Sciurus vulgaris*) destroy many of the cones in which the larvae live to get the seed. Other much less important predators include willow tits (*Parus montanus*) which occasionally eat the larvae, and great spotted woodpeckers (*Dendrocopus major*) and crossbills (*Loxia curvirostra*), both scarce in Thetford Chase, which eat pine seed in winter and so must destroy a few *conicolana* larvae incidentally. A very few cones ($<0{\cdot}1\%$ in 1956 and 1957) were eaten by larvae of *Dioryctria* sp. No other predator on the cones or on *conicolana* was recognized in Thetford Chase; though several

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species of birds and probably some small mammals eat the pine seeds once the cones have opened in spring. The *conicolana* larvae are parasitized by the ichneumonid *Ephialtes laticeps* Ratz. (Betts 1958); and there will doubtless be various other, as yet unrecognized, causes of mortality of *conicolana*. The predation by tits on the larvae of *conicolana* is peculiarly amenable to quantitative investigation because the numbers of the predators, and both the density of the prey and the proportion destroyed, are comparatively easily measured in the field. It will be shown that the tits leave characteristic traces on the cones of their attacks on the larvae; and that these traces can be distinguished from the emergence holes of the moths, and the emergence holes of the moths from those of the parasites (cf. Reichart 1957).

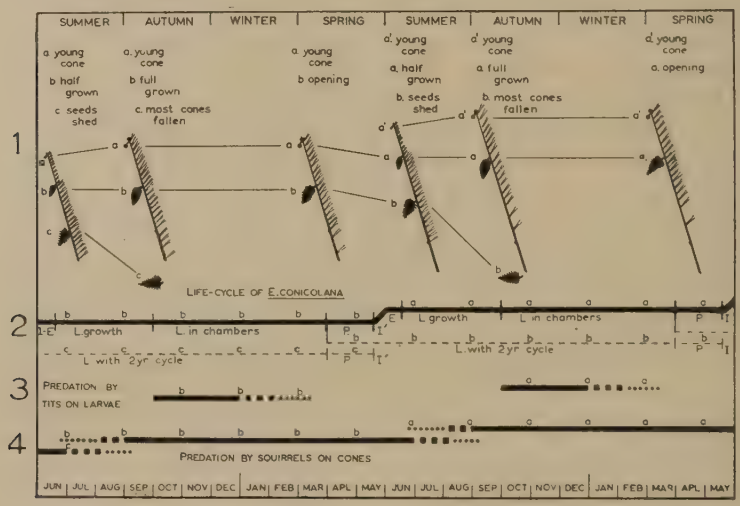

Fig. 1. Diagram to show the timing of (1) successive stages in the growth of scots pine cones, (2) the life cycle of *Ernarmonia conicolana* (I, imagines, E, eggs, L, larvae, P, pupae), (3) the predation by tits on *conicolana* larvae in the cones, (4) the predation by red squirrels on the cones.

Different generations are labelled a^1, a, b, and c; the cones in which *conicolana* lives and on which the tits and squirrels feed are indicated by the appropriate letter repeated above each band. All dates are approximate.

Samples of the cones were examined from about twenty localities in Thetford Chase following two winters. It was found that the larvae of *Ernarmonia conicolana* were most unevenly distributed over Thetford Chase as a whole, and similarly within a single forest compartment which was investigated in greater detail, and that the severity of the tits' predation was related to the abundance of the larvae. The position of the larvae in the cones and the number of larvae per occupied cone also affected the tits' predation. The squirrels' predation on the cones was measured by counting the stripped butts of cones dropped by them on to permanent square-metre plots. The density of the squirrels was not measured.

A. Part of cone cut away to show *conicolana* pupa in its chamber; the larva spends the winter in the same position.

B. Lower row of 4 cone-scales: emergence holes of *conicolana*, with partly extruded pupal case and moth on extreme right. Upper row of 3 cone-scales: the smaller emergence holes of the larval parasite, the ichneumonid *Ephialtes latiiceps* Ratz. Note that the emergence holes of the moth are all close to the tip of the scale, while those of the ichneumonid are variously situated.

C. Side view of empty pupal case, after emergence of the moth, partly extruded from the emergence hole in the tip of the cone-scale. Note that the flap over the emergence hole has already half closed across the pupal case, the extruded part of which will probably break off at this point.

D–F. Typical traces of attacks by tits on *conicolana* larvae (see Table 4). D. Hole in centre of scale. E, Double hole in right scale attacked, and enlarged emergence hole in left scale attacked. F, Two scales fully ripped open.

The smallest divisions on the scale (the same for all photographs) are 0·5 mm. (*Photographs by the author*)

(*Facing page 377*)

THE BIOLOGY OF *ERNARMONIA CONICOLANA*

The larvae (Betts 1958) are found most commonly in scots pine cones. The eggs are laid in June, singly on the surface of one-year-old cones that are due to shed their seed in the following spring, and as soon as they hatch in early July the larvae burrow in to the seeds, on which they feed until about September. There are usually only one or two larvae in each occupied cone, though up to eight were recorded (Table 8). On the average each larva eats about seven seeds in its lifetime (Table 1). In late September or October the fully-fed larva eats its

Table 1. *Consumption of seeds of scots pine by larvae of* Ernarmonia conicolana

The cones examined were collected from three trees at Bacon's Strip in the spring of 1956. The mean oven-dry weight of 100 sound seeds was 720 mg; sound seeds from occupied and unoccupied cones were of similar weight. The fresh weight of a full-grown larva is about 7 mg.

Number of cones examined	200
,, ,, ,, occupied by *conicolana*	84
,, ,, larvae per 100 cones	61·7
,, ,, ,, ,, occupied cone	1·5
,, ,, sound seeds per unoccupied cone	32·4
,, ,, ,, ,, ,, occupied cone	21·7
,, ,, ,, ,, eaten per larva	7·3
Percentage of sound seeds eaten by larvae	
... in all cones	14·7
... in occupied cones only	33·1

way from the seeds to the surface of the cone, where it excavates a chamber in which it spends the winter and eventually pupates in March (Pl. 3). The chamber is protected from the outside only by a thin layer of cone cuticle, and the larva lines its chamber with silk shortly before it pupates. Before pupating, too, the larva weakens the periphery of the future emergence hole to assist emergence, leaving part of the cuticle intact as a hinge. The moth emerges in late May or June. As it emerges the pupa is partly extruded through the emergence hole (Pl. 3), and the extruded part of the pupa often breaks off later, allowing the flap of cone cuticle to close and making the chamber hard to see.

When a cone hangs naturally from a pine branch, part of it is almost hidden against the branch and part is fully exposed facing away from the branch. It is usually easy to see which way round a cone picked up from the ground had hung on the tree, because the stalk enters the cone obliquely and because the scales on the outer face of the cone are better developed than those on the inner face. When the cones were examined in 1956 and 1957 each chamber was assigned to one of twelve 30° longitudinal segments; the results given in Table 2 have been grouped in four 90° segments. The chambers of *conicolana* were distributed unevenly round the cones. In 1956 and 1957 combined, about one-third of the 4087 chambers recorded were in the outer quarter and about one-fifth in the inner quarter of the cone. The reason for this is unknown, but perhaps the seeds in the outer quarter are the largest and provide the best feeding for the larvae; it may also be relevant that larvae in the outer quarter tend (significantly, $\chi^2 = 12{\cdot}1$) to pupate before those elsewhere, and that the parasites are concentrated on larvae in the inner quarter (Table 2).

In the autumn of 1956 a small proportion of the chambers in the fallen cones still contained *conicolana* larvae which had failed to pupate in the previous spring. These late larvae were not parasitized and in fact pupated and moths emerged from them in the following spring from cones kept indoors over the winter of 1956-57, but (Betts 1958) they might not have survived in nature. There was a slight, but significant ($\chi^2 = 5{\cdot}86$) tendency for these larvae to be in cones with more than one chamber, and since Betts (1958) found that *conicolana* pupae from cones containing three or more pupae tended to be under weight, it seems that larvae in one cone may compete with each other for food. It was thought possible that these late larvae might have spent the previous winter in the centre instead

Table 2. *The position of* E. conicolana *in the cones: 1955-56 and 1956-57*

The cones for the winter of 1955-56 were examined in the autumn of 1956, after most of the moths had emerged; those for 1956-57 were examined in the spring of 1957, before any moths had emerged. The delayed larvae found in the autumn of 1956 were those with a two-year life-cycle.

1955-56	Percentage distribution				Percentage of all chambers attacked by tits
Quarter of cone	Emergence holes	Delayed larvae	Attacked chambers	All chambers	
Outer	28	27	37	33	62
Inner	21	21	12	16	42
Left	26	24	27	26	56
Right	25	28	24	25	54
Total recorded	868	155	1248	2271	–

1956-57	Percentage distribution					Percentage of all chambers attacked by tits
Quarter of cone	Larvae	Pupae	Parasites	Attacked chambers	All chambers	
Outer	20	31	14	36	31	59
Inner	30	23	34	12	19	32
Left	24	21	23	27	25	56
Right	26	25	29	25	25	50
Total recorded	310	525	56	929	1820	–

of in their chambers near the surface of the cones and that this might have accounted for their delayed pupation, but their distribution round the cone agreed with that of the emergence holes only, rather than with that of the whole population prior to the tits' predation (see p. 389), so they had presumably been subjected to the tits' predation and were therefore already in their chambers during the winter of 1955-56.

In the rather early spring of 1957, the imagines of the ichneumonid parasite on the *conicolana* larvae emerged from the cones towards the end of March, some eight weeks before the moths. The emergence holes of the parasite are noticeably smaller than those of the moths (about 0·7 mm across compared with about 1·5

mm) and are less consistently in the same position on the cone-scale (Pl. 3). It seems that parasitized larvae do not always burrow to the extremity of the scale. Since unparasitized larvae fully excavate their chambers in autumn, the parasites must attack the larvae before this stage. As the next generation of *conicolana* does not reach the surface of the cones until the September or October following the parasite's emergence, the parasite could have a second generation in another species of host during the summer, but this is not known.

Table 2 also shows that in the spring of 1957 about 6% of all the larvae were parasitized, but that the parasites were somewhat concentrated on the inner quarter of the cone ($\chi^2 = 4{\cdot}63$). Thus 8·1% of the larvae in the inner quarter were parasitized, but only 3·5% of those in the outer quarter. The characteristic emergence holes of the parasite had not been positively identified when the cones for 1956 were examined, but it was obvious that the proportion of larvae parasitized in 1955-56 was not much different from that in 1956-57.

BEHAVIOUR OF TITS FEEDING ON *E. CONICOLANA*

Blue and coal tits feed on the larvae of *conicolana* from October to early March (Fig. 1 and Table 3), and many were identified in the birds' gizzards. Compared with coal tits, blue tits with their shorter and stouter bills are better adapted for

Table 3. *The density and feeding behaviour of blue and coal tits in scots pine plantations, 1952-57*

Figures show the number of tits per 100 ha, and in parentheses the percentage of those feeding that were searching for *conicolana* larvae.

		Sept.-Oct.	Nov.-Dec.	Jan.-Feb.	Mar.-Apr.
1952-53	Blue	- (11)	- (14)	- (15)	- -
	Coal	- (0)	- (3)	- (1)	- -
1953-54	Blue	43 (0)	44 (5)	37 (0)	16 (0)
	Coal	113 (1)	112 (6)	102 (1)	83 (0)
1954-55	Blue	58 (4)	24 (9)	16 (15)	3 -
	Coal	203 (1)	157 (9)	83 (6)	70 -
1955-56	Blue	48 (12)	58 (49)	49 (60)	13 (17)
	Coal	150 (0)	123 (36)	110 (30)	76 (16)
1956-57	Blue	76 (5)	58 (53)	48 (6)	21 (0)
	Coal	185 (0)	150 (3)	156 (1)	154 (0)

hacking out the larvae from the tough cones. Correspondingly field observations showed that blue tits spent longer than coal tits searching for *conicolana*, except in the winter of 1953-54 when all insect food including *conicolana* was very scarce.

Tits searching for *conicolana* visit many cones in quick succession: on the average, blue tits spend about 5 sec per cone and coal tits perhaps a little longer. It is evidently more profitable for them to examine many cones cursorily than fewer cones carefully. Exactly how the tits locate the hidden larvae is uncertain. There is normally no indication to our eyes of the presence of the chambers, though exceptionally the flap of cuticle covering the future emergence hole is slightly paler than the surrounding tissue. Blue tits almost always tap each scale with the bill

to locate *conicolana*. If the tip of the bill struck the flap over the future emergence hole, the larva would certainly be revealed, but the emergence hole is only about 1·5 mm across, and though it is usually in about the same position on each scale (Pl. 3), it is hard to believe that the bird relies on striking it to find the larva. Possibly a cone scale with a chamber hollowed out in its tip may sound or feel different from other scales wherever it is tapped; on the other hand it is unlikely that a chamber in one scale could be detected by tapping an adjacent scale. Coal tits too sometimes tap the scales, but unlike blue tits they also seem to peer at the cones without tapping, perhaps looking for discoloured flaps over the chambers. The movement of the bird's head when it taps is so slight that it was at first uncertain in the field whether it was in fact tapping the cone. But this searching behaviour of blue and coal tits was watched not only in the field but also in an aviary at a distance of less than 1 metre, where the cones were strung on taut wires attached to the wire-netting cage. When the tits tapped the cones the noise resounded on the wires.

Table 4. *Frequency of types of traces left by tits on scots pine cones after extracting larvae of* E. conicolana

	Percentage frequency
Pseudo-emergence hole	3
Enlarged emergence hole	19
Hole in centre of cone scale	15
Hole at base of cone scale	36
Cone scale fully ripped open	21
Double hole in cone scale	6

After finding a larval chamber a blue tit will rip it open and extract the larva with such dexterity that it is sometimes extremely difficult, even in an aviary, to appreciate that this is what it has done, whereas the coal tit with its finer bill must often hack at the cone for several seconds to get the larva. In order to distinguish whether chambers of *conicolana* broached by tits could be reliably distinguished from chambers from which moths had emerged, a sample of cones was examined in March and April, after the tits' predation but well before the moths had emerged. The types of traces left by the tits are listed in Table 4 and illustrated in Pl. 3. About 97% of the traces left by the tits were at once distinguishable from the emergence holes of the moths, while the remaining 3% (the pseudo-emergence holes of Table 4) could have been confused at first sight with genuine emergence holes. However, since the larvae line their chambers with silk just before pupation, chambers attacked by tits are unlined and genuine emergence holes lined. A genuine emergence hole also contains the head capsule and shrunken skin of the larva, shed on pupation, and sometimes the posterior part of the pupa.

From aviary experiments it seemed that there was no consistent difference between the traces left by blue tits and those by coal tits; in particular, both species sometimes ripped the chambers fully open. In the field only coal tits were seen making double holes, and they too may have been responsible for the few

pseudo-emergence holes from which larvae could have been more easily extracted with a fine bill than with the blue tit's conical one. Double holes and pseudo-emergence holes were not recorded in the aviary. My interpretation of the double-holed trace is that the chamber was first detected through the future emergence hole, towards the extremity of the scale, and the larva then extracted through the hole nearer the base of the scale, either to prevent the larva from escaping or because it had already partly withdrawn. The larva can retreat from its chamber a little way down the channel leading up to it, where it gets some protection from overlapping cone scales; it cannot retreat further because the channel is blocked by its own excreta. Should a larva be attacked unsuccessfully it spins a silken cap across the freshly exposed end of its chamber, so when cones are examined in March and April the number of chambers attacked successfully and unsuccessfully can be counted. In a sample of 474 attacked chambers examined in March and April 1956, only four (0·8%) had been attacked unsuccessfully, and each of these had been attacked successfully on a later occasion. In another sample of 567 attacked chambers examined in March and April 1957 fourteen (2·5%) had been attacked unsuccessfully and still held larvae or pupae.

DENSITY OF *E. CONICOLANA*

Some preliminary measurements of the density of *conicolana* and of the tits' predation on them were made following the winters of 1952-53, 1953-54 and 1954-55, but this account is primarily concerned with the winters of 1955-56 and 1956-57. The absolute density of *conicolana* in terms of the number per unit area of forest depends on the density of cones as well as on the number of larvae in them. The latter measurement is here called the 'intensity', following Morris (1955), and is expressed as the number of *conicolana* per 100 cones. The density and intensity of *conicolana* may vary independently from year to year, because the crop of cones is highly variable. The density of the cones and hence also of *conicolana* was measured in one locality, Bacon's Strip, for the winters of 1954-55, 1955-56 and 1956-57. The cone crop seemed to vary similarly from year to year over the whole of Thetford Chase, with minor local variations. The size of the cone crop at Bacon's Strip for the winters of 1954-55 and 1955-56 was measured by counting the cones falling on to 205 square-metre plots in the scots pines, and on to 125 similar plots in the Corsican pines. The plots were permanently laid down at about 10 m intervals along transect lines, and were inspected and cleared of cones every month or two. Besides the number of whole cones, the number of stripped butts of cones dropped by the squirrels was also counted.

Most of the cones that have shed their seeds in one spring fall to the ground during the summer and early autumn of the same year, but some are retained on the trees for several years and cannot be dated when they appear on the plots, though they are recognizably old. These old cones formed 18-19% of the total fall in 1955 and 1956 (counts for 1957 were incomplete). Thus an estimate of the crop for any one year based on the number of cones known to belong to that year plus

Table 5. *Details of cones examined in Thetford Chase*

All counts were in plantations of scots pines, except the single count in Corsican pines at Bacon's Strip for 1955-56 given at the end of this table. The area of the main block of scots pines, planted in 1933, at Bacon's Strip was 72 ha (178 acres), consisting of nine forest compartments. Bacon's Strip was subdivided into two approximately equal areas for the counts for 1955-56 and 1956-57. Counts elsewhere were made in single compartments of about 6-10 ha (15-25 acres) at each locality.

E = emerged, L = Larvae, P = Pupae, and Ps = Parasitized larvae.

	Year planted	No. of cones		Survivors		No. of *conicolana* eaten by tits	Intensity (chambers/ 100 cones)	Eaten by tits (%)
		Examined	Occupied	E.	L.			
WINTER 1955-56								
40-acre Plantation	1933	150	63	23	6	63	61	69
Brickkiln Farm	1935	200	80	26	3	96	63	77
Gravelpit Wood	1935	200	87	47	7	86	70	61
Devilsdyke Wood	1934	250	63	34	4	43	32	53
Bacon's Strip N.	1935	200	56	35	5	52	46	57
Bacon's Strip I	1933	600	260	80	13	113	34	55
Bacon's Strip II	1933	300		63	7	75	48	52
Heath Farm	1929	200	38	22	5	16	22	37
Methwold I	1933	150	115	25	2	32	39	54
Methwold II	1933	200		34	5	73	56	65
Warren Lodge	1927	200	47	30	5	20	27	36
Cranwich Heath	1932	200	26	17	3	14	17	41
Mundford Covert	1929	250	71	40	3	45	35	51
Great Covert	1929	200	37	24	8	18	25	36
West Tofts Belt	1927	225	35	25	3	15	19	35
Mousehall	1926	210	28	26	1	15	20	36
Bromehill Cottage I	1927	500	48	33	6	18	11	32
Santon Square	1928	205	23	29	2	1	16	3
Halfmoon Plantation	1928	225	25	21	1	6	12	21
Shakers Road	1926	350	33	19	7	9	10	26
Croxton Heath	1936	325	48	25	9	29	19	46
WINTER 1956-57				L.+P.	Ps.			
40-acre Plantation	1933	100	39	14	0	46	60	77
Brickkiln Farm	1935	100	26	11	2	17	30	57
Gravelpit Wood	1935	116	47	35	1	30	57	46
Devilsdyke Wood	1934	100	43	38	0	27	65	42
Bacon's Strip N.	1935	100	31	29	0	16	45	35
Bacon's Strip I	1933	435	266	59	0	104	38	64
Bacon's Strip II	1933	444		101	2	134	53	56
The Oaks	1946	100	47	29	1	39	69	57
Weeting Heath N.	1933	100	38	23	0	19	42	45
Cranwich Heath	1932	100	16	16	0	1	17	6
Windmill Covert	1929	100	62	43	8	54	105	52
Mundford Covert	1929	100	57	40	4	55	99	56
Mousehall	1926	100	11	14	0	1	15	7
Bromehill Cottage I	1927	100	26	20	1	17	38	45
Bromehill Cottage II	1927	45	38	71	4	40	256	35
Bromehill Priory	1945	100	55	58	1	49	109	45
Bromehill Plantation	1925	100	28	15	0	14	29	48
Santon Square	1928	100	1	1	0	0	1	–
Halfmoon Plantation	1928	100	61	45	8	43	96	45
The Square	1928	100	52	32	4	30	66	45
Clump Heath	1928	100	15	15	0	1	16	6
Chimney Plantation	1924	100	84	54	7	122	183	72
Warren Wood	1925	100	14	9	5	2	16	12
Shakers Road	1926	100	57	41	9	50	100	50
Croxton Heath	1936	100	26	14	0	15	29	52

Miscellaneous counts	Winter	Year planted	No. of cones examined	Intensity: (chambers/ 100 cones)	Eaten by tits (%)
Bacon's Strip	1952-53	1933	211	73	50
	1953-54		195	9	23
	1954-55		1360	8	55
Shakers Road	1954-55	1926	500	4	50
Croxton Heath	1954-55	1936	500	6	54
Weeting Heath*	1954-55		400	3	15
Bacon's Strip: Corsican pines	1955-56	1933	200	22	5

* Scattered trees >100 years old.

those from previous years will certainly be less, and probably very much less, than 20% out, and the tendency will be to overestimate a small crop and underestimate a large one. This method of estimation was impracticable for the winter of 1956-57 because the field-work had to be finished before the autumn of 1957. The cone crop at Bacon's Strip that year was therefore measured by counting all the cones on 105 trees of mean girth, and multiplying the average number per tree by the density of the trees. This may involve small errors, as trees of average girth may not be strictly representative of the whole plantations in the number of cones they bear, although such trees are known to be representative in several other respects.

The number of *conicolana* per hundred cones and the proportion of them eaten by the tits were measured by examining the cones and counting the number of emergence holes, or larvae and pupae, and the number of chambers successfully attacked by tits. This was normally done in the autumn following the winter in which the tits' predation occurred, by which time at least three-quarters of the cone crop had fallen to the ground. Cones still retained on the trees have the same density of emergence holes and attacked chambers as those on the ground. The usual practice was to pick up five cones every ten paces along two or more transect lines in each forest compartment sampled; the cones examined were thus truly representative of the areas covered.

The counts for the winter of 1956-57 were made in late March and early April instead of in the following autumn, and the cones were picked from the trees as they had not yet fallen to the ground. The samples of cones examined in 1957 were neither so large nor so representative of the forest compartments concerned as in previous years, because of the time taken to climb sufficient trees and because the cone crop was exceedingly sparse in most localities. In the autumns of 1953, 1954 and 1955 the fallen cones were simply examined as found. It was realized later, however, that this incurred a slight risk of overlooking emergence holes across which the flaps had closed after the moths emerged (see p. 377). So in the counts for 1955-56 and 1956-57 after the chambers attacked by tits had first been counted all the cones examined were shaved with a knife to disclose emergence holes. The figures for the earlier years are thus a little less reliable than those for the two later years.

PREDATION ON *E. CONICOLANA* BY TITS

(*a*) *The level of predation*

Table 5 shows that in four of the five winters at Bacon's Strip the tits ate between 50% and 65% of the population of *conicolana* larvae, and in one winter about 23%; and that the average proportion eaten over Thetford Chase generally was about 45% in both 1955-56 and 1956-57. Such a consistently heavy predation by birds has rarely been recorded for any animal prey (cf. references in Lack 1954,

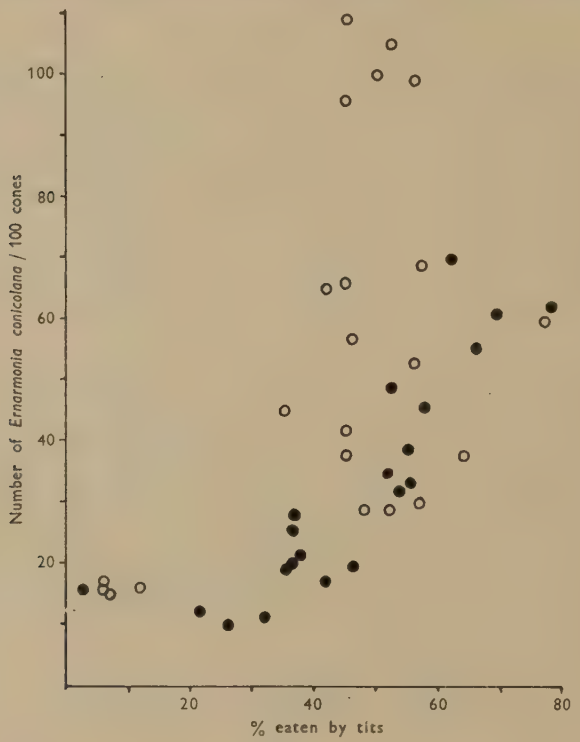

Fig. 2. Predation by tits and the intensity of *E. conicolana* in the winters of 1955-56 (●) and 1956-57 (○). Two extreme points have been omitted for 1956-57; Bromehill Cottage II (intensity 256, 35% eaten) and Chimney Plantation (intensity 183, 72% eaten)—see Table 5.

ch. 13; also Reinhart 1957); it is nevertheless in line with estimates for other insect prey made concurrently with the present study and in the same area. The smaller proportion of *conicolana* larvae eaten at Bacon's Strip in the winter of 1953-54 could be explained by the greater abundance of alternative insect food available then than in other winters.

The two winters studied in special detail differed in that the cone crop was exceptionally heavy in 1955-56 and exceptionally light in 1956-57 (Table 9). The

tits' predation was conspicuously 'intensity dependent' in the first winter, but hardly at all in the second (Figs. 2 and 3). In the winter of 1955-56 the tits ate about 25% of the *conicolana* in areas with low intensities of 10-15 larvae per hundred cones, about 50% with medium intensities of 30-40 larvae per hundred cones, and about 70% with high intensities of about 65 larvae per hundred cones. The number of live *conicolana* larvae per hundred cones ranged from about 10 to 70 at the beginning of the winter, and from about 7 to 25 at the end of the winter when the tits had ceased feeding on them (Figs. 2 and 3). The tits thus reduced a highly variable population of *conicolana* to a more uniform level over the whole of Thetford Chase; the intensity dependence of their predation was striking.

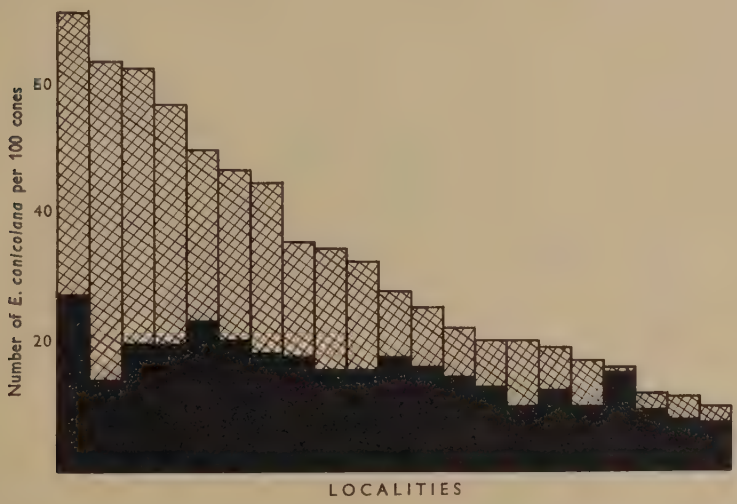

Fig. 3. The number of *E. conicolana* larvae per hundred cones before (full columns) and after (black) predation by tits in the winter 1955-56. Each column represents one locality in Thetford Chase; they are arranged in descending order of the intensity of the larvae.

In the winter of 1956-57 the intensity of *conicolana* was generally higher than in the previous winter, but their absolute density was very much less because there were so few cones (Table 10). At low intensities of about 15 larvae per hundred cones the tits ate a correspondingly small proportion of about 10%, but between the intensities of about 17 and 30 larvae per hundred cones there was a marked threshold, above which the tits ate some 50% of the larvae. Within the very wide range in intensities of from 30 to 256 larvae per hundred cones there was no suggestion of any intensity dependence in the tits' predation (Fig. 2).

The proportion of the population of *conicolana* larvae eaten by the tits will depend on how quickly the birds can find the larvae. This will in turn depend on the absolute density and intensity of the larvae; it is also influenced by the number of larvae per occupied cone, the position of the larvae in the cones, and perhaps

by the choice of alternative foods. It is reasonable to suppose that with a normal crop of cones the intensity of *conicolana* will be more important to the tits than the density, since the cones are conspicuous whereas the larvae in them are not. But the density of the larvae may become more important when the crop of cones is very sparse, as it was in 1956-57. While the intensity of the larvae may normally be the more important factor determining the proportion of the larvae that the tits eat, their absolute density will determine how long the stock of larvae will last.

An intensity-dependent predation such as occurred in 1955-56 implies that the tits found the larvae more easily the higher the intensity of the larvae; this is readily understandable. An intensity-independent predation as in 1956-57 implies similarly that the tits could not find the larvae more easily the higher the intensity; this is absurd unless some other factor offsets the otherwise clear advantages to the tits of a high intensity of larvae. Now Table 6 shows that at Bacon's Strip in

Table 6. *The relationship between the density of cones, the density and intensity of* conicolana *and the predation by tits: Bacon's Strip, scots pine, 1956-57*

The trees sampled were all of mean girth (35 ± 2 cm at breast height) and were at a density of about 2510 trees/ha.

Cones per tree	Number sampled		Density (larvae/ 10 sq. m)	Intensity (larvae/ 100 cones)	Eaten by tits (%)
	Trees	Cones			
1- 5	29	63	4	73	71
6-14	13	111	12	59	
15-29	10	222	26	47	59
>29	10	691	60	36	

Note the negative correlation between the density and the intensity of *conicolana*, and the positive correlation ($\chi^2 = 5{\cdot}58$) between the intensity of *conicolana* and the proportion eaten by tits.

1957 the intensity of the larvae was highest where the density of cones, and so also of the larvae, was lowest. Hence the advantage to the birds of a high intensity of larvae may have been offset by their low density. An approximately even rate of predation over a wide range of intensities was thus understandable with so small a crop of cones as in 1956-57. While this is the most likely explanation of the lack of intensity-dependence in the tits' predation in the winter of 1956-57, it has not actually been proved correct, and another possible explanation must be considered before being rejected.

At Bacon's Strip there was two or three times as much other insect food in the foliage of the scots pines in the mid-winter of 1956-57 as in 1955-56; on the other hand, there were only 32 *conicolana* larvae per 10 sq. m of forest in the autumn of 1956, compared with 152 larvae per 10 sq. m in 1955 (Table 10). Consequently, *conicolana* formed only about 4 % of the total stock of insect food in the pine foliage in November and December 1956, compared with about 25 % of the smaller stock in 1955. This meant that in the winter of 1956-57 *conicolana* larvae were an important food of blue tits in November and December only, and were seldom eaten by coal tits, whereas in 1955-56 they were an important food of both blue and coal tits from November to February inclusive (Table 3).

The tits' predation was independent of the intensity of *conicolana* in 1956-57 and this could have been accounted for had the larvae been such an unimportant food that the blue tits never searched for them specifically, but merely ate those that they happened to find whilst really searching for other foods. But this was not so, for no less than 53 %, of all the blue tits watched feeding in November and December 1956 were searching for the larvae. Moreover birds searching for other foods will not often find *conicolana* accidentally, because the larvae are the only accessible food in the cones in winter and are in any case normally hidden from view. Thus the tits must have a very real 'search image' (Tinbergen 1949 and in press), though not necessarily a visual image of *conicolana* larvae to find them at all frequently.

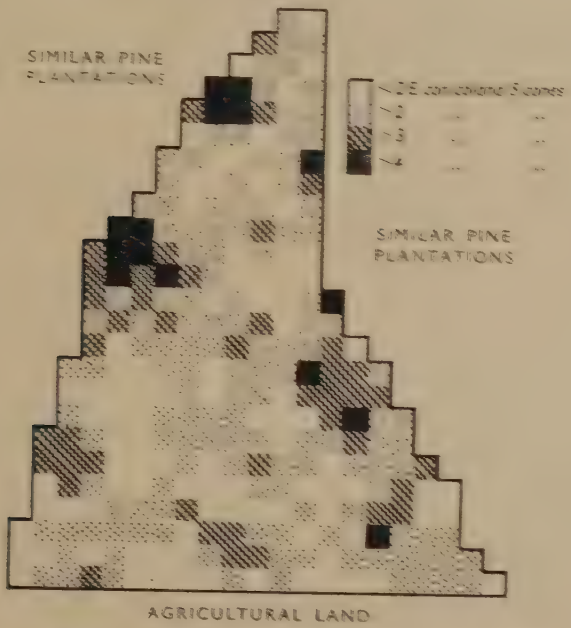

Fig. 4. Map of a forest compartment of 6·5 ha (16 acres) of scots pines at Bacon's Strip to show the uneven distribution of *E. conicolana*. Five cones were examined from each 15 × 15 m square. The base line is 315 m long.

Bacon's Strip differed from most other localities in Thetford Chase in 1956-57 by having rather more cones: in March 1957 it was quite easy to find cones there, whereas none at all was found in many other localities. Presumably as a result of this, the tits' predation on *conicolana* was intensity-dependent within Bacon's Strip in 1956-57 (Table 6), though not so over Thetford Chase as a whole. Since in 1956-57 areas with a high intensity of *conicolana* larvae had a low density, the tits' predation was negatively density-dependent.

(*b*) *Predation within one forest compartment*

It is clear from Table 5 and Figs. 2 and 3 that *conicolana* was unevenly distributed over Thetford Chase, the number of larvae recorded per hundred cones ranging from 10 to 70 in 1955-56 and from 1 to 256 in 1956-57. In 1955-56 the intensity of the larvae was higher towards the western edge of Thetford Chase than elsewhere, but no such trend was discernible in 1956-57. In the autumn of 1956 a detailed examination of the distribution of *conicolana* within one forest compartment at Bacon's Strip (Fig. 4) revealed wide fluctuations in their intensity within this comparatively small area. The compartment was roughly triangular in outline and sloped gently from its northern apex down to its southern base. The eastern and western sides adjoined similar scots pine plantations, while the southern edge bordered agricultural land. The compartment was divided into squares by a 15 m

Table 7. *The relationship between the intensity of* conicolana *and the proportion eaten by tits within a single forest compartment of 6·5 ha. (c. 16 acres): Bacon's Strip, scots pine, 1955-56*

Larvae per plot of five cones	Equivalent intensity (larvae/100 cones)	Number of: Plots sampled	Number of: *conicolana* recorded	Eaten by tits (%)
1- 2	31	125	192	53
3- 5	73	97	353	62
6-10	145	15	109	66

grid, and five cones were examined from each of the 283 squares so formed. Figure 4 shows that there were well-marked pockets of high and of low intensities of *conicolana* of varying size, which formed an irregular pattern within the compartment. The boundaries between pockets of high and of low intensity were sometimes abrupt, sometimes gradual, and the intensity of the *conicolana* larvae was neither especially high nor especially low along the edges of the compartment. Even within this one compartment the proportion of *conicolana* eaten by the tits increased with their increasing intensity, though not quite so steeply as between different compartments (Table 7, cf. Fig. 2).

(*c*) *The number and position of larvae in the cones*

Table 8 shows that, in general, the more *conicolana* per cone the greater the proportion of them taken by the tits, and that this was somewhat more marked the higher the intensity of the larvae. This suggests that when a tit finds a larva in a cone it searches the rest of that cone more carefully than it would otherwise have done, presumably because there is then an especially good chance of finding more than one larva per cone, particularly at high intensities. There are two apparent exceptions in Table 8 to this general trend, the first group of 1955-56 and the last of 1956-57. The former is not statistically significant and may be disregarded. The latter is based on a collection of only forty-five cones from a single tree with an exceptionally high intensity of *conicolana*: the proportion of

the larvae eaten from cones with four or more chambers (28%) was significantly lower than in other groups with ordinarily high intensities. The intensity of *conicolana* in this one tree was much greater than in neighbouring trees (256/100 cones compared with 26/100 cones; see Table 5). It seems that the tits continued to search this tree as if the *conicolana* were at the same intensity on it as on other trees near by; they would not then have expected to find many cones with more than three or four larvae in each.

Table 8. *The relationship between the number of* conicolana *larvae per cone and the proportion eaten by tits: 1955-56 and 1956-57*

1955-56				1956-57			
Intensity groups	Larvae per cone	Cones sampled	Larvae eaten (%)	Intensity groups	Larvae per cone	Cones sampled	Larvae eaten (%)
1-16	1	109	22	15-18	1	50	6
	2	17	14		2	7	14
	3	3		25-50	1	344	54
17-30	1	205	35		2	106	54
	2	41			3	32	
	3	11	45		4	9	61
	4	2			5	2	
31-49	1	323	50	51-75	1	117	53
	2	97	57		2	41	54
	3	25			3	12	
	4	4	62		4	6	67
	5	1		95-110	1	157	38
50-70	1	213	61		2	86	53
	2	93	68		3	32	
	3	30			4	15	
	4	6	85		5	1	63
	5	3			6	1	
				183	1	33	48
					2	23	66
					3	16	
					4	6	
					5	5	78
					6	1	
				256	1	10	
					2	10	50
					3	6	
					4	4	
					5	4	
					6	2	28
					7	1	
					8	1	

It has been shown in Table 2 that the *conicolana* larvae were concentrated round the outer, exposed quarters of the cones. Whatever the reason for this distribution, the tits ate a higher proportion of the larvae from the outer than from the inner quarters of the cones, so that almost equal numbers of larvae survived from each quarter (Fig. 5). Thus the tits again concentrated their attack where the larvae were most numerous and where they were presumably most easily found. Apart

in on the fact that a higher proportion of the larvae were parasitized on the inner than on the outer quarters of the cones (see Table 2). It is not known if the tits selected either for or against parasitized larvae or even for that matter if the larvae are already parasitized when the tits eat them.

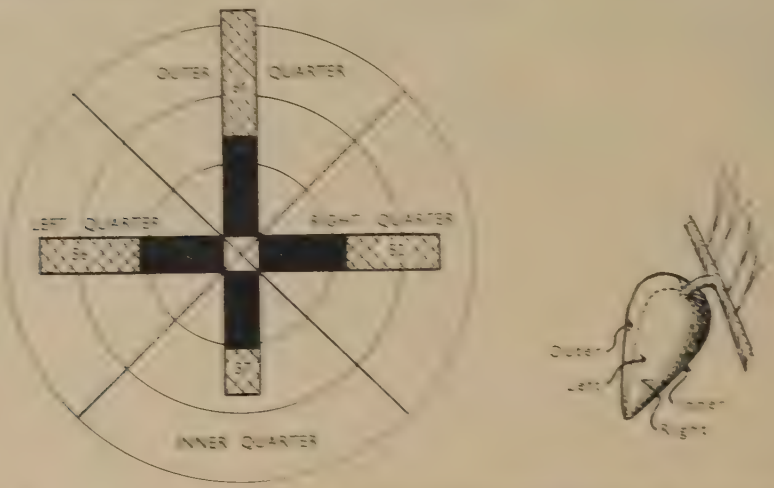

Fig. 5. The distribution of *E. conicolana* in the four quarters of the cone before tits' attacks, and after blocked in predation by tits. Thetford Chase, 1955-56 and 1956-57 combined. The figures in the hatched areas are the percentages of the larvae eaten by the tits. The sketch shows the four quarters of the cone.

PREDATION ON *E. CONICOLANA* BY SQUIRRELS

Pine seed is a staple food of red squirrels all the year round in Thetford Chase, and they destroy about the same number of cones each month (Fig. 6). The squirrels deal with the cones with impressive skill and can completely strip a cone in about 45 sec, though about 90 sec per cone is more usual. Butts of cones stripped by grey squirrels (*Sciurus carolinensis*) are pictured by Shorten (1954), and those stripped by red squirrels are similar.

So far as is known the red squirrels selected neither for nor against cones containing *conicolana*, though a single cone found in the spring of 1957 bore four neat tooth marks of a squirrel, each one slicing off the tip of a cone scale, two of which had contained *conicolana*. To obtain a given quantity of seed, the squirrels would have to destroy rather more cones when the intensity of *conicolana* was high than when it was low, to compensate for seeds already eaten by the larvae. By the end of September 1955 at Bacon's Strip, when there were 39 *conicolana* per hundred cones, the larvae had eaten about 10% of the initial stock of seeds. At the end of May or in June, the squirrels began eating the ripening cones due to shed their seeds in the following spring, and for a time ate both these and late cones left from the previous spring. By about August or September they had completely switched

to the fresh crop of cones (Fig. 1). In a normal spring the seeds of scots and Corsican pines are shed from about the end of March onwards. In assessing the squirrels' impact on the cones, the initial crop was taken as the number of one-year-old cones present at the end of May, and the final crop those surviving at the end of the following March, *i.e.* the initial crop for 1957 was that present at the end of May 1956, and the final crop that left by the end of March 1957.

The initial and final crops of cones for 1955, 1956 and 1957 at Bacon's Strip, and the number of cones destroyed by the squirrels, are given in Table 9. In the

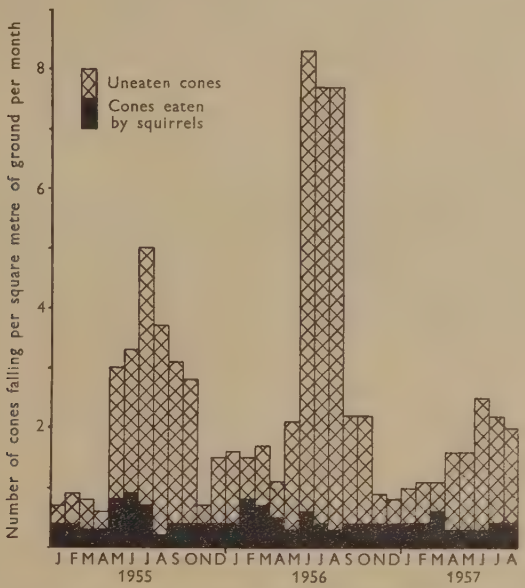
Number of cones falling per square metre of ground per month
8
6
4
2
Uneaten cones
Cones eaten by squirrels
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
1955
1956
1957

Fig. 6. The numbers of scots pine cones falling naturally to the ground, and of butts of cones dropped after being stripped by red squirrels; monthly from January 1955 to August 1957, at Bacon's Strip.

scots pines, the number of cones destroyed has varied surprisingly little in the three years, considering that the initial crops have ranged from seven to thirty-nine cones/sq. m, and the proportions of these destroyed from 16% to 65%. Clearly the squirrels could not have maintained this rate of consumption had the crop been much less than it was at Bacon's Strip in 1957; indeed elsewhere in Thetford Chase they effectively cleared the whole of the meagre crop in that year. The population of squirrels was not measured, but in years with an ordinary density of cones their numbers are probably not limited immediately by food shortage, though they may be so limited when the cone crop is as small as it was in the winter of 1956-57.

At Bacon's Strip the area of Corsican pine is only about one-fifth that of scots pine, and the number of cones produced per unit area of plantation is quite insignificant compared with the scots pine. But the squirrels seem to prefer

Corsican to scots pine seed, and in each of the last three years (details for only two years in Table 9) they have eaten most of the Corsican pine cone crop.

DISCUSSION

The efficiency with which the tits sought out and exploited those places in which *coniciana* was most readily found was a remarkable and significant feature of their predation. This has been demonstrated at every stage. The intensity- or density-dependence of their predation in 1955-56 and the lack of it in 1956-57 are both explained in these terms, whether widely separated localities or adjacent 15 m plots are compared, and whether the distribution of the larvae in different quarters of the cones or the number of larvae per occupied cone are considered.

Table 9. *The size of the crops of cones and the numbers eaten by red squirrels at Bacon's Strip: 1955-57*

Figures represent numbers of cones per sq. m of ground. 150 sq. m plots were examined in the scots pines and 125 in the Corsican pines. Estimates are based on the fall of cones in 1 m trees inside the plantations only: edge trees bear more cones/sq. m but are so much in the minority that they do not significantly affect total production in a large forest area. Crops were not measured in earlier years but were reckoned heavy in 1953 and light in 1954.

The initial crop is that of ripening cones on 1 June of the previous year: the final crop refers to the number of ripe cones ready to shed seed on 1 April of the years given.

	Initial crop	Eaten by squirrels: Number of cones	Eaten by squirrels: Percent of initial crop	Other losses*	Final crop
SCOTS PINE					
1955	26·8	6·0	22·4	0·7	20·1
1956	39·2	6·1	15·6	0·6	32·5
1957	7·2	4·7	65·4	0·8	1·7
CORSICAN PINE					
1955	0·55	0·51	92·7	0·02	0·02
1956	0·20	0·16	80·0	0·01	0·03
1957	–	–	–	–	–

* Includes many cones picked by squirrels, but dropped uneaten.

These are not mere slight tendencies, but examples of almost perfect intensity- or density-dependent predation. Such efficiency is, incidentally, further evidence of the over-riding importance of the search for food in the lives of small birds in winter (*cf.* Gibb 1954, 1956).

Blue and coal tits begin to feed on *coniciana* as soon as the larvae become accessible in their chambers in autumn, and will presumably continue to feed on them until there are so few larvae left that it is more profitable to look for other foods. This stage is evidently reached by about January in most winters, but later when the larvae are as numerous as in 1955-56 (Table 3). The exact date must depend on the density of the tits, on the density and intensity of the larvae, and on the amount of alternative food available. Though the proportion of the *coniciana* population that the birds have eaten by the end of the winter will depend in the last resort on their efficiency in finding them, the proportion eaten

will also vary with the density and intensity of the larvae and inversely with the amount of alternative food. The density of the birds, on the other hand, will probably not greatly affect the proportion of the larvae eaten, but only the date at which they turn to other foods. Since, as Table 10 shows, the density and intensity of *conicolana* larvae and the amount of alternative food in the pine foliage at Bacon's Strip varied markedly from one winter to another, it is perplexing that the tits ate consistently between 50% and 60% of the larvae in four of the five winters. Although the tits' predation was strongly dependent upon the intensity of the larvae within 1955-56, it was evidently not so comparing different years. As already suggested (p. 384), the reduced predation by the tits on *conicolana* in 1953-54 could be attributed to the great weight of alternative insect food available in the autumn of 1953.

Table 10. *Some factors affecting the proportion of the population of* conicolana *larvae eaten by the tits in scots pines at Bacon's Strip*

The data for 1952-53 and 1953-54 are less adequate or complete than those for the later years, but are included for rough comparison. The dry weights of other insect food exclude *conicolana* larvae. The larvae of *E. conicolana* formed about 12% of the weight of all the insect food in the pine foliage in November and December 1954, 25% in 1955 and 4% in 1956.

	1952-53	1953-54	1954-55	1955-56	1956-57
Density of *conicolana* larvae in October (larvae/10 sq. m)	–	–	22	152	32
Intensity of *conicolana* larvae in October (larvae/100 cones)	73	9	8	39	45
Mean dry weight of other insect food in scots pine foliage in November and December (kg/10 ha)	–	55	3	14	13
Density of blue and coal tits in November and December (birds/10 ha)	–	16	18	18	21
Percentage of *conicolana* larvae eaten by the tits in winter	50	23	55	54	60

Tinbergen (1949 and in press) found that tits ate a relatively smaller proportion of certain lepidopterous larvae in summers when the larvae were very numerous than when they were less numerous (*cf.* Betts 1955). He attributed this to the birds' supposed preference for a mixed diet. Probably *conicolana* were never so abundant in Thetford Chase that the birds turned away from them in this way. In any case alternative insect food is seldom so plentiful in pine plantations in winter that a tit can afford to neglect one food for another simply in order to vary its diet, no matter how desirable this might be. Although, in any one year, areas with a high intensity of larvae may have a low density (Table 6), on the average over a long term of years, ignoring the vagaries of the cone crops, winters with a high intensity will also be those with a high density of larvae. Hence, if the proportion of *conicolana* eaten by the tits is normally intensity-dependent, it will seem also to be density-dependent. This assumes that the density of *conicolana* and that

of the cones are unrelated from year to year, which is probably so at most ordinary densities of cones, although the numbers of *conicolana* may well be limited by such very low densities of cones as in 1956-57. Squirrels, on the other hand, may normally be density-independent destroyers of *conicolana* larvae, provided that they neither select nor reject occupied cones. They may, however, destroy a particularly large proportion of the larval population in those, perhaps rare, years when the scarcity of cones limits the density of the larvae.

Until much more is known about other causes of mortality among *conicolana*, especially at other stages in their life cycle, and about their reproduction, further discussion of the possible effects of the tits' and squirrels' predation, and of the density of the cones, on the population of *conicolana* is too unrealistic to be rewarding.

The destruction of pine seed by *conicolana* larvae and by squirrels is economically unimportant in Thetford Chase. The larvae will rarely eat more than a small proportion of the available seed, and it is normal forest practice to collect cones required for seed in the autumn before they are due to shed, that is before the squirrels have taken their toll but after the larvae are fully fed.

ACKNOWLEDGMENTS

It is a pleasure to acknowledge my debt to those who have contributed to this study. My colleague Dr Monica Betts first identified *Ernarmonia conicolana* in Thetford Chase and later found the larvae in the birds' gizzards; she helped to plan the programme and discussed its progress from day to day. Mr D. D. B. Summers also helped to plan the programme and assisted in the field from 1954 to 1956, and Mr R. Creed was a great help in the field in the spring of 1957. Dr David Lack, F.R.S., and Dr Betts (Edward Grey Institute, Oxford), and Dr K. Wodzicki and Mr J. S. Watson (Animal Ecology Section, D.S.I.R., Wellington) all read the manuscript and made many helpful suggestions for its improvement. I am most grateful, too, to Dr L. de Rutier of Groningen University for letting me read the important manuscripts of the late Professor L. Tinbergen before they were sent to the press. The research was done under the auspices of the Nature conservancy, and the Forestry Commission allowed us to work in Thetford Chase.

SUMMARY

1. The observations described in this paper were made in the pine plantations of Thetford Chase, East Anglia, from 1952 to 1957 (chiefly 1955 to 1957).

2. The larvae of *Ernarmonia conicolana* (Heyl.) (Lepidoptera: Eucosmidae) spend the winter and pupate in chambers just beneath the surface of cones of scots pines (*Pinus sylvestris*) and, less often, of Corsican pines (*P. nigra*). Blue tits (*Parus caeruleus*) and coal tits (*P. ater*) prey upon the larvae in winter; while red squirrels (*Sciurus vulgaris*) destroy many of the cones in which the larvae live, to eat the seed. The larvae are also parasitized by the ichneumonid *Ephialtes laticeps* Ratz.

3. The tits leave characteristic traces on the cones which can be distinguished from the emergence holes of the moths, and those of the parasites.

4. The populations of *conicolana* larvae were measured and recorded in terms of the number per unit area of forest (density) and of the number per given number of cones (intensity). The crops of cones were also measured.

5. The *conicolana* larvae were unevenly distributed within Thetford Chase and the tits' predation upon them was compared in different localities. The tits ate about 45% of the populations of larvae each winter. In one winter with a very heavy crop of cones the tits' predation was strikingly dependent upon the intensity of the larvae reaching 70% where this was high. In another winter with a light crop of cones the tits' predation was hardly 'intensity-dependent' at all.

6. Within one forest compartment of 6·5 ha the tits' predation was still influenced by differences in the intensity of the larvae from one part of this compartment to another.

7. There are usually one or two (occasionally up to eight) larvae per occupied cone. In general, the more larvae per cone, the greater the proportion eaten by tits.

8. The larvae were concentrated on the outer quarter of the cone, exposed as it hangs on a branch, and the tits ate a greater proportion of these larvae than of those on the hidden quarter of the cone. Consequently the surviving larvae were almost evenly distributed round the cones. A rather greater proportion of the larvae on the inner than on the outer quarter of the cone is parasitized, but fewer than about 5% of all the larvae were parasitized in each of two years. It is not known if the tits select for or against parasitized larvae.

9. Since the proportion of the larval population of *conicolana* eaten will depend on the efficiency of the individual bird, which will continue to prey upon them so long as it remains profitable to do so, the density of the tits need not affect the proportion of the larvae eaten, but will determine how long the stock of larvae will last.

10. The efficiency with which the tits exploited those places and situations in which they could find the larvae most readily was a significant feature of their predation, and the intensity- or density-dependence of their predation are explained on these grounds.

11. The number of cones eaten by red squirrels was measured. In three years the initial crops of scots pine cones ranged from 7 to 39 cones sq. m of forest, of which the squirrels ate from 16% to 65%. The initial crops of Corsican pine cones were 0·2 and 0·6 cones sq. m in two years, of which the squirrels ate 80% and 93%. The population of squirrels was not measured.

12. It is concluded that the tits may normally be density-dependent predators, and the squirrels density-independent predators, on the *conicolana* larvae; but it is not yet possible to assess their effects on the population of *conicolana*.

13. The destruction of pine seed by *E. conicolana* larvae and squirrels is economically unimportant in Thetford Chase.

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REVIEWS

AMERICAN PALAEOECOLOGY

Harry S. Ladd (Editor) (**1957**). *Treatise on Marine Ecology and Paleoecology:* Vol. II. *Paleoecology*. Pp. x—1077; 36 plates; 97 text-figures. New York: The Geological Society of America (Memoir 67). Price $10.00.

Eighteen years ago one of the pioneers of palaeoecology, Dr T. Wayland Vaughan, organized a subcommittee within the Geologic Research Committee of the National Research Council of America to explore the possibilities of producing a collective treatise on those aspects of marine ecology and palaeoecology particularly related to palaeontology. Under the chairmanship of Harry S. Ladd a panel of contributors have produced a two-volume treatise, the first on Marine Ecology (Editor: Joel W. Hedgpeth) and the second on Paleoecology (Editor: Harry S. Ladd).

This second volume is divided into three main sections. The first, misleadingly named 'The Paleontological Record and the Origin of Life', contains most of the material in the volume which will be of use to ecologists. It contains three admirable chapters by Harry S. Ladd on the palaeontological record (historical account of the interpretation of fossils, types of fossilization and replacement, etc.), the nature of palaeoecological evidence (evidence from the fossils themselves and the rock which contains them, including a review of some recent techniques for interpreting physical conditions of ancient seas) and, with Gordon Gunter, a historical account of the development of marine palaeoecology. Elso S. Barghoorn contributes a very useful review of the main pathways along which ideas on the origin of life are travelling, and examines some of the more cogent evidence of precambrian organisms. The organic constituents of fossils are dealt with by Philip H. Abelson, who points out that amino acids have been found in fossils, some as old as 360 million years, which may yield the possibility of a geological thermometer for sediments. Each chapter in this useful section has a comprehensive bibliography.

The greater part of the volume is taken up by the second section containing selected analyses from the geological record of what is known of the palaeoecology in U.S. deposits. The contributions have been governed more by the availability of authorities than the need for a particular section, though there is an assurance in the foreword that the committee and its collaborators discovered several blank areas in the field and initiated investigations into them. The majority of Chapters 7-21 are of specific interest to American geologists only, but the final two chapters of the section contain summaries of intensive work on single localities. The first (Ladd *et al.*, on the bays of the central Texas coast) shows how the distribution of distinct faunal facies seem there to be controlled primarily by salinity. The second (Bradley on Sagadahoc Bay, Maine) is an interesting account of a comparison between present-day conditions in a single locality and those reflected in the sub-fossil shells which underlie them; the chapter also emphasizes the features of the present-day situation which would be difficult to interpret in a geological sediment.

The third section is devoted to an annotated bibliography of works with a palaeoecological slant arranged systematically.

The concept of producing a comprehensive treatise bringing together so many facets of ecology was a bold one, and the result is excellent; one is made aware throughout of the shortcomings as well as the immense potentialities of modern palaeoecology, and British workers in this field will be sorry that there is yet no comparable volume covering the British column in as comprehensive a manner. The treatise as a whole would be

even more useful if the American committee would bring out a third volume dealing particularly with the palaeoecology of past animals by comparison with modern close relatives.

DAVID NICHOLS

EAST AND WEST

C. H. Lindroth 1957. *The faunal connections between Europe and North America.* Pp. 334; 72 text-figures. New York: Wiley; Stockholm: Almqvist & Wiksell. Price 120s.

It is impossible to be certain what happened ten or twenty thousand years ago, for which reason zoogeography tends to attract those who enjoy armchair theorizing unhampered by excessive factual detail. Lindroth is not of this company and builds on a rock-like foundation of fact: he has been twice to Iceland and twice to Newfoundland and the relentless pursuit of relevant detail has brought him to this country in search not only of biological but of historical material as well. In this he has been undeterred by the broad west country accents in which the ancient mariners whom he sought out doubtless addressed him or by the seventeenth-century English of the port documents that he wished to peruse.

A comparison of the faunas of two continents must be based on groups that have been studied by a taxonomist familiar with both, which means that the different branches of the animal kingdom will be very unevenly represented. In such groups about 17% of the total there are 908 common species, and the listing of them with notes on the range of each takes up pp. 17 to 124. Lindroth soon concluded that a number of species had been introduced and that, in order to find out how, he must learn more about early shipping connections and the carriage of ballast. The result of this study is presented first.

If early Norse visits left any effect on the fauna it cannot now be traced. Cabot rediscovered Newfoundland in 1497, whereafter it became a fishing ground for English seamen, who discouraged settlement for fear that a permanent colony might interfere with their activities. Not till 1750 did the settled population reach any size. The presumption that ships bound for a virtually uninhabited land would travel in ballast was confirmed by a study of records in various west-country ports from Poole round to Bristol, and other information came to light too. It was, for example, forbidden to tip ballast over the side on arrival, lest the harbours should be filled up, and it had to be brought ashore, a regulation that had far-reaching faunistic results. Lindroth was able to discover the actual ballast-gathering grounds at several ports and collect on them. 50% or more of species in the groups studied had been found also in America, and by comparing these with the species known only in Europe, Lindroth reaches conclusions about the way of life likely to favour transportation.

Fewer immigrants from America to Europe, most being aquarium or hot-house species, the author attributes mainly to the nature of the cargoes carried, but sets forth an alternative explanation. Cultivation started in Eurasia and plants have had several millenia in which to adapt themselves to the conditions which it provides. In America, when Europeans first went there, cultivation was rudimentary at best and non-existent along the western seaboard. Accordingly, when man started clearing and cultivating European 'weeds' and animals associated with them, brought over unintentionally, could establish themselves with no competition from native species. Plants or animals coming to Europe on the other hand, generally found no unoccupied niche and failed to gain a foothold.

Of the species unlikely to have been carried by man, there is a group that tends to be restricted to Europe and the eastern side of America. Sixteen are strong-flying

sea-birds, sixteen Lepidoptera belonging to families noted for their powers of flight and twenty-one are spiders, all balloonists. Probably these animals occasionally or frequently cross the Atlantic today. One sponge and four plants have probably been transported by birds blown across the Atlantic. For one animal only, an ant, does Lindroth fall back on the conventional explanation that it is a species which has remained unchanged for a very long time, surviving only in parts of a great area in which its range was once continuous.

Finally, Lindroth turns to those animals whose present range can be explained only in terms of prehistoric events. The fauna of Iceland is largely, that of Greenland to an unexpected extent, European, whereas in Baffin land no European species have been found. This leads the author to abandon the idea of a recent connection between Europe and America though he produces evidence of a land-bridge across the Bering Strait, open, however, only at a time when cold-tolerant species could cross it. If land masses drifted apart in the way that Wegener postulated, this happened so long ago that any effect on the fauna is no longer detectable.

A land connection from Europe to Greenland, on the other hand, is a conclusion difficult to avoid. Such a bridge would deflect the Gulf Stream from Scandinavia and produce a cold climate there, colder than the one which subfossil remains indicate existed during the last interglacial phase and since the Ice Age. The land bridge has therefore to be put back to the last inter-glacial period but one, which means that the present-day inhabitants of Iceland and Greenland have had to survive two glaciations. Possibly the Gulf Stream would maintain a temperate climate along the coastal fringe of such a bridge but it is suggested that refuge areas were created by the hot springs that are a feature of Iceland today. In Scandinavia short-winged specimens of a beetle preponderate in what are believed to be the refuge areas of Norway, whereas only long-winged forms occur in Sweden and Finland. In Iceland the highest proportion of brachypters is found in the neighbourhood of the hot springs, which does support the suggestion that these were refuge areas.

The whole approach in this book is sound. The author writes (p. 279) 'Speculations founded exclusively on maps of distribution, as now often happens, do not give satisfactory results'; animals for him are not dots on a map but living creatures with habits which must be known and which differ from species to species. Aware, moreover, that it is uncommon to find two species with identical ranges and that few countries even in Europe have been explored fully, he approaches with caution those groupings of animals which some writers find so fascinating. There are a few unimportant errors such as 'insect rests' for 'insect remains' (p. 271) and 'unevitable' for 'inevitable' together with one or two other unusual words, some of which may be the recognized form in America, and the very strict would prefer 'owing to' in many places where 'due to' is used, but in general the book is written in clear and correct English. Indeed it compares favourably with many written by British-born authors. The basic data are fully presented and there are many pages of lists and tables. Numerous distribution maps are in the old-fashioned lavish style with a picture of the animal inset. The photograph of *Little Minnie*, a two-masted topsail schooner built in 1866 at Padstow, and various others, add a welcome decorative touch, but luxuries, alas, are always dear in these times, and the price is likely to mean that many who would like to possess the book will borrow it.

T. T. MACAN

Richard H. Pough (1957). *Audubon Western Bird Guide*. Pp. xxxvi+316: 32 coloured plates: 138 text-figures. New York: Doubleday. Price $4.95.

This is the third bird guide produced by Richard Pough for the National Audubon Society, the two earlier volumes describing the birds of eastern North America. The area

covered by the book is vast and extends from Bering Strait, through Canada along the eastern side of the Rocky Mountains, and then south roughly through the middle of the States to the Mexican border. Some 614 species are dealt with, of which only 208 are exclusively western and it is these that are figured and described in detail here: the remainder are fully described in the eastern guides and only their ranges are given in this volume. There are 32 plates of good coloured illustrations in the middle of the book and numerous line drawings of birds in flight in the text. The descriptions vary in length from half to two pages, with paragraphs on identification, habits, voice, nest and range.

This strikes me as a thoroughly well-produced book easy to use and giving just the information which is wanted in a guide which is truly of pocket size.

P. F. HOLMES

O. E. Wynne (1956). *Key-list of the Palaearctic and Oriental Passerine birds.* Pp. 134. Arbroath: Buncle. Price 15*s.* 6*d.*

This list was first published as six parts in the *North Western Naturalist* between 1953 and 1955, and it has been reprinted as this small book, with revisions and three appendices. As explained in his preface the author decided some twelve years ago to make a count of the number of different birds in the world, and in doing this he found that there were no convenient modern lists of the Passerine birds of the Palaearctic and Oriental regions. This key-list is an attempt to fill the gap. It is not meant to be a check-list in the normal ornithological sense, since this would have made it too bulky a publication. Against each species is given only the general breeding range (such as E. Palaearctic or Malaysia) and the vernacular name, with no reference to the original description; under this are given the races, with authors and dates. There is unfortunately no indication of the range of the races, except that they are listed from N.W. to S.E. in each case.

Appendix A gives a list of the full names of authors of the names of birds mentioned in the work, with the dates of births and deaths and reference either to where they worked or to a biographical notice. This somewhat unusual information has its uses for those of us who may be quite familiar, for example, with the abbreviation 'Vieill.' after a bird name, but not with L. J. P. Vieillot (1748-1831). Of the other two appendices, one gives a list of recent books and the other is an index to genera and subgenera.

This key-list will undoubtedly be a reliable work of reference, though I cannot agree with the publishers who claim that every naturalist's library should have a copy. For a book which is destined mainly for reference libraries, it is a pity that it has only been bound in uncovered boards, making rebinding essential before it can be put on the shelves.

P. F. HOLMES

THE INSECT WORLD

T. W. Kirkpatrick (1957). *Insect Life in the Tropics.* Pp. xiv + 311; 146 text-figures (drawings and photographs). London: Longmans Green. Price 35*s.*

It is the abundance and diversity of tropical insects that make a book describing their natural history so much in demand, yet at the same time so difficult to write. Professor Kirkpatrick, an enthusiastic field entomologist with a wide experience in East Africa, the West Indies, Egypt and the Sudan, is obviously well qualified to tackle such a formidable task, and he has produced a fascinating and scholarly book which will, I predict, remain the standard work of its kind for many years to come.

His book is addressed to those, not primarily trained entomologists, who show an

interest in 'general natural history'. For such readers, especially those who are actually living in the tropics, it will undoubtedly be both useful and entertaining. But it also provides something of unusual value for the general biologist, an introduction to one of the most widespread of animal groups through its tropical representatives. It is inevitable, but none the less paradoxical, that most students of ecology should become acquainted first of all with examples from the highly specialized and impoverished fauna of temperate regions, and only secondarily, if they are fortunate, with those from the tropics. Such a reversal of biological emphasis is, of course, particularly regrettable where poikilothermous animals are concerned. It is from this point of view, perhaps more than any other, that this book must be regarded as providing a valuable introduction to insect natural history.

The preliminary section consists of a short chapter describing the principal characteristics of the tropical environment (this being defined as the region between the tropics of Cancer and Capricorn), a chapter on insect structure, and one on classification.

The main part of the book is concerned with various aspects of insect natural history, the subjects of the seven remaining chapters being development, reproduction, locomotion, food and feeding habits, defence and protection, insect architecture, and insect communities. Each chapter is a well-argued survey, illustrated by numerous and pertinent examples. In selecting these, the author has tried to avoid re-quoting facts about well-known insects of agricultural or medical importance, and instead cites examples from less familiar species, drawing where possible from his own experience. Such treatment, as the author points out, has resulted in a large proportion of the examples being from East Africa or Trinidad.

An outstanding feature of the book is the illustrations. These consist of line drawings and photographs, each with an easily comprehensible scale. The drawings, on glossy paper, set a high standard in entomological textbook illustration, and are well chosen to bring out the points made in the text; they are large, and make excellent use of stipple-shading and, where appropriate, scraper-board. Numerous figure and page references in the text make very good use of the available examples, and there is a well-arranged subject index.

PHILIP S. CORBET

Kurt Harz (1957). *Die Geradflügler Mitteleuropas.* Pp. xxiii + 494; 20 coloured plates; 255 text-figures. Jena: Fischer. Price DM 69.20.

This is a handbook of the Orthoptera of central Europe, taking the group broadly to include four orders—the Stick Insects do not occur within the faunal limits. All but one or two of the British species are mentioned. The work is primarily systematic, with keys for the identification of the genera and species. This part is useful for anyone working in central Europe but the illustrations are not of the highest quality though usually adequate. Each order is introduced by an account of its morphology and of its general biology. There is a very full discussion of song in grasshoppers and crickets, especially with reference to its function in pairing and in species-separation. Under each species there are short notes on general habitat and geographical distribution, and (where appropriate) song. The information on natural enemies, particularly parasites, is much less satisfactory. Quite a number of well-known parasites seem not to be mentioned but as no Latin names other than those of Orthoptera are indexed it is difficult to be sure. The literature, more particularly the German literature, is reasonably well dealt with up to 1953; after that date, no doubt unavoidably, there are many omissions. There is some evidence that the non-German literature has not been fully digested, *e.g.* Matthey's

work on the cytology of *Saga* is cited in the literature but nothing is said about it under the genus. In some respects also the literature is treated too narrowly. Some of the striking American work on the pairing of Mantidae ought to be mentioned: there are a good many short biological notes in the British literature which would have helped to complete the biological accounts. It is a book which an ecologist would find useful as a source of information though not primarily written for him.

O. W. RICHARDS

TWO TAXONOMIC KEYS

D. J. Scourfield & J. P. Harding (1958). *A Key to the British Species of Freshwater Cladocera.* Pp. 55: 111 text-figures. Ambleside: Freshwater Biological Association (Sci. Publ. no. 5. 2nd ed.). Price 4s. 6*d*.

The revision of the Freshwater Biological Association Scientific Publication No. 5 has been undertaken by Dr J. P. Harding. The key does not differ greatly from the earlier edition. The genus *Daphnia* however, has been brought up to date by the addition of two species, *D. curvirostris* and *D. ambigua*, known to occur regularly in the south of England. The third addition in this genus, *D. carinata*, must be regarded as a very doubtful member of the British fauna. Many students of limnology have great difficulty in distinguishing between *D. longispina* and *D. hyalina* when the latter species occurs without the typical pointed crest on the head. This difficulty arises from failure to understand what is implied by the term 'crest'. It is a pity that this point has not been clarified in this revised edition.

Dr Harding is to be commended for the improved arrangement of the figures and ecological notes. These are now interspersed in the relevant places in the text of the key, thus much time is saved and the work of identification greatly facilitated. This revised and improved edition of a publication already well established and widely used will be invaluable to all those interested in the British freshwater fauna.

B. M. GILCHRIST

H. B. N. Hynes (1958). *A Key to the Adults and Nymphs of British Stone-flies (Plecoptera).* Pp. 86: 43 figs.: 30 maps. Ambleside: Freshwater Biological Association (Sci. Publ. no. 17). Price 5*s*. 6*d*.

Dr Hynes's revised and enlarged keys to the British Plecoptera will be of great value to all students interested in our stoneflies. Since the first edition was published in 1940 two additional species have been recorded from Britain and considerable changes in nomenclature have unfortunately been necessary. The present edition covers a wider field, in that keys to the nymphs are given as well as to the adults.

The main part of the work is of course devoted to the keys to the families, genera and species, but there is a useful introductory section dealing with structure, classification, collecting and ecology; the distribution of most of our species on a vice-county basis is covered by thirty maps. In the keys under each species, details are given of the time of occurrence of the adult, its degree of rarity and the type of habitat in which it breeds. The work is well illustrated with line-drawings and as far as possible the illustrations have been arranged to face the appropriate section of the key.

In the section on nomenclature, it is possible that some students may be a little confused by the list of changes of name. It would have been clearer if, for example 'Taeniopteryx Pict. = Nephelopteryx Klap.' had been given as 'Taeniopteryx Pict.

replaces *Nephelopteryx* Klap.' Taxonomists will of course understand that the first name replaces the second, but these keys will go into the hands of many people unacquainted with taxonomic procedure. It should also be pointed out that it is not *Rhaidiopteryx neglecta* (Albarda) but the mis-identified *Rh. neglecta* of British authors which is a synonym of *Rhabdiopteryx anglica* Kim. These are, however, minor criticisms and the author and the Freshwater Biological Association are to be congratulated on producing such a useful addition to the Association's series of Scientific Publications.

D. E. KIMMINS

A NEW JOURNAL

Entomologia Experimentalis et Applicata, Vol. 1 (1) (1958). Pp. 72. Amsterdam: North-Holland Publishing Company. Price £3 3*s*. per volume.

This journal is edited by three Dutch biologists, one French, one German and one British (Dr K. Mellanby of Rothamsted). In a disarming foreword they write: 'Starting a new journal is always a difficult and controversial undertaking. There are so many existing publications that most research workers are already overwhelmed by them . . . On the other hand the results of painstaking original work may have to wait too long before they are published . . .' As a further *raison d'être*, they claim that the contacts between experimental and applied entomology have formerly been too restricted. It can of course be argued that instead of adding new journals we should enlarge the present ones and clarify the scope of each, or that a more highly centralized system of publication is necessary. Meanwhile, in the absence of a settlement of these broad questions, the task of publication becomes greater year by year, and a new journal such as *Ent. exp. & appl.* deserves to be welcomed and supported. Its scope, although wide, is fairly clearly defined: it will include papers concerned with experimental aspects of the biology and ecology, pure and applied, of 'insects and other land arthropods', but not purely descriptive ecology. Drastic condensation is requested.

The first issue consists of papers from a Symposium on Insects and Foodplants held at Wageningen in 1957. The result is presumably not typical of what the editors plan, inasmuch as these articles are mainly brief reviews or résumés of work described in full elsewhere. Seven deal with aspects of foodplant selection by insects and of host-resistance (four of them deal specifically with the Colorado Beetle, two with aphids). There is a review on the nature and function of salivary secretions in plant-sucking Hemiptera, and a paper on the dietetics of a blowfly. Five papers are in English, including three by Dutch and German authors; three are in German, with English or French summaries; and the ninth in French.

M. E. SOLOMON

ECOLOGY IN NEW ZEALAND

Proceedings of the New Zealand Ecological Society, Nos. 3 and 4. Reports of the fourth and fifth annual meetings, 1956 and 1957. Pp. 35 and 46. Wellington: New Zealand Ecological Society. Prices 3*s*. and 7*s*. 6*d*.

Both numbers follow the same pattern. The business is disposed of on the inside of the cover and the reports on the exhibits and excursions are of equally commendable brevity. There is no statement of accounts nor indication of strength. The first six pages of No. 3 are devoted to the presidential address, which is on the training of ecologists. Six contributions to a symposium on the ecology of tussock grasslands fill the next eleven pages and the discussion a further three. A second symposium, on habitat classification,

with four speakers and discussion, occupies another seven pages and four papers unrelated to the symposia the remaining six. The overall impression is of a lively and vigorous society.

Ecology is at an early stage of development in New Zealand and much of the work will probably follow lines established elsewhere. Moreover the descriptive ecology of parts foreign to them is rarely of interest to ecologists. On the other hand general relationships and principles may arouse universal attention. Therefore, proceedings in their present form will commend themselves to the overseas reader, who can see almost at a glance what is going on and can quickly decide whether there is anything about which he would know more. The shop-window display is well done but the counter service is not so good; the inclusion of titles in references would be well worth the extra space and careful checking would save the customer annoyance. The paper on which the symposium of habitat classification is based appeared in the *Journal of Ecology*, not the *Journal of Animal Ecology* as stated.

T. T. MACAN

LABORATORY ANIMALS

A. N. Worden & W. Lane-Petter (Editors) (**1957**). *The UFAW Handbook on the Care and Management of Laboratory Animals.* Pp. xix+951; numerous illustrations. London: UFAW. Price 70*s*.

Some people, like Dr Johnson, are so preoccuccupied with morbid thoughts of death that the subject has become an obsession with them, and further, some of these unfortunates anthropomorphically attribute similar fears of death to animals. True, 'life is sweet, Brother' and no normal person wishes to take his departure before the will to live is lost, and doubtless the animals enjoy living as far as they can consciously enjoy anything apart from a vague background feeling of euphoria. But death in itself can have no meaning for any animal, and provided it comes swiftly it is of no consequence to the rest of the world whether any one of the millions of animals lives or dies, although 'not a sparrow falleth to the ground without His notice'. The attitude of the sentimentalists is quite illogical: can it matter ethically whether twenty or two hundred mice are used in an experiment? Is living in one cage among a thousand in an animal house preferable for a mouse to not living? How many animals survive from each litter or brood in the wild to reach maturity?

It is fortunate that a movement which was started many years ago to protect the interests of animals has been guided away from the path that leads to inverted sadism and emotional anti-vivisection propaganda into more sensible channels, mainly by the devoted work of Major C. W. Hume, and has now produced a volume that can only be described as the animal-experimenter's bible. Everyone agrees that on humanitarian grounds alone the animals used in experimental work must be given every reasonable care and attention, and must be subjected to no more physical distress than is absolutely necessary in attaining results of genuine importance. The volume under review gives the fullest advice on the methods by which these essential conditions may be attained. It is a large book of nine hundred and fifty pages, and is the composite work of nearly ninety contributors—it reflects the greatest credit upon its editors whose task must have been enormous.

The first part of the book deals with general aspects of animal management such as housing, feeding and breeding, and many other matters; it incorporates a vast amount of research, and presents the most up-to-date recommendations on the husbandry of laboratory animals. The modern animal house must be maintained on hygienic lines as strict as those in any hospital, and nutritional requirements must be studied even more

carefully than those of farm animals. It is of great importance to the experimenter that his animals should be as uniform as possible in all their characters, and the chapters on the breeding and maintenance of pure lines are packed with valuable information on these matters.

In the second part the various species are dealt with individually, and a chapter is devoted to each of the more important ones. Practically everything that is known about the care of laboratory stocks of rabbits, guinea pigs, mice, rats, dogs, cats and all other usual laboratory mammals are here collected and collated. In addition there are numerous chapters about mammals that are less familiar in experimental laboratories, at least in this country, and the management of some very interesting species is described. In addition to the mammals, large sections of the book are devoted to various birds, reptiles, amphibians and fishes. But that is not all—several species of invertebrates are dealt with at considerable length, and shorter notes are given about many other kinds of animals that may be required for special investigations.

The first edition of this work appeared ten years ago, and the large size of this edition compared with that of its predecessor shows what a vast amount of information on the management and welfare of laboratory animals has accumulated in that short space of time. It is difficult to say which should be most grateful to UFAW for producing this excellent and invaluable handbook—the laboratory animals or those who use them as a foundation for a successful career in biology.

L. HARRISON MATTHEWS

A BIOLOGIST'S ESSAYS

F. S. Bodenheimer (1957). *Studies in Biology and its History.* Vol. I. Ten essays. Pp. 146; 4 plates; 8 text-figures. Jerusalem: Biological Studies. Price $6.00.

This volume includes certain purely factual papers, a translation of a Hebrew version of part of a work by Aristotle, and an impressive bibliography of Professor Bodenheimer's 394 contributions. As the ten items have no particular unity, the present review will be mainly concerned with one of the few articles which can really be called an essay, and one of the research reports to which it has some relevance. The essay, 'Knowledge and Biology', while paying proper tribute to Aristotle's greatness, advances the more dubious thesis that a closer study of his works would be the best means of hastening a reform in biological principles. It may be true that Aristotle has contributed more ideas to biology than anyone else has, and the fact that many of them are false is unlikely to impede progress in the twentieth century as did Aristotelian cosmology in the Middle Ages. Nevertheless it is arguable that, if time can be found in an overcrowded curriculum, it should be given to a study of the quantitative and experimental philosophy which led to the overthrow of Aristotelianism. Too many ideas in population ecology already seem to be based on Aristotelian rather than Galilean views about the structure of a scientific system, and one can at least make out a case that this is an unsatisfactory state of affairs. Indeed Professor Bodenheimer's choice of an example to illustrate a successful advance in knowledge (Siivonen (1955) 'Population fluctuations and the lunar cycle') suggests that he is prepared to accept a hypothesis on its ingenuity rather than on empirical criteria.

There is also an odd discrepancy between what Professor Bodenheimer says in 'Knowledge and Biology' and the course he follows in practice. In the essay he stresses the indivisibility of the complex of animal and environment; elsewhere he explains the difference in longevity between voles in the laboratory and in nature solely in terms of the additional risks from the so called 'non-physiological component of destruction'.

Yet his assumption is that 'physiological survival rate' is an attribute which has some meaning independently of environmental conditions of temperature, humidity, diet and numerous other factors whose effects are inseparably bound up with the measurement of longevity. In the case of fertility, by contrast, Professor Bodenheimer does not hesitate to attribute the lower values observed in the field to the influence of physical factors.

Professor Bodenheimer regards as highly unsatisfactory the statement by Bertrand Russell that 'all human knowledge is uncertain, inexact, and partial', but might well recognize that the truth of this doctrine is often illustrated by those who claim to have discovered a full explanation for some natural event. His warning in another essay against losing sight of the assumptions involved in supraorganismic theories in synecology shows that it is easier to be critical of other people's ideas than of one's own. The present review does not pretend to be an exception.

DENNIS CHITTY

BOOKS RECEIVED

Environment of New Zealand Pleuston Populations by KAJ WESTERGV. New Zealand Department of Internal Affairs, Wildlife Publication No. 40B. 1956.

On the Dynamics of Exploited Fish Populations by R. J. H. BEVERTON & S. J. HOLT. London: H.M.S.O. 1957. (MAFF Fish. Invest. [2] 19.) Price 126s.

General Zoology by MARY J. GUTHRIE & J. M. ANDERSON. New York: Wiley. 1957. Price 60s.

The Physiology of Insecta. Vol. II. *Behaviour*. Edited by MARGARET E. BROWN. New York: Academic Press. 1957. Price $14.00.

Proceedings of the New Zealand Ecological Society. No. 5 (Report of Sixth Annual Meeting, August 1957). Wellington: N.Z. Ecol. Soc.

Treatise on Marine Ecology and Paleoecology. Vol. 1. *Ecology*. Edited by JOHN W. HEDGPETH. New York: Geol. Soc. of America, Memoir 67. 1957. Price $12.50.

Common Names of British Insect and Other Pests. Compiled by L. THOMAS & H. W. JANSON. London: H.M.S.O. 1957. (MAFF Technical Bulletin No. 6.) Price 7s. 6d.

Pests and Pests of African Crops. Prepared by N. R. JOSHI, E. A. McILWAINE & R. W. PHILLIPS. FAO, Rome, 1957; London: H.M.S.O. 1958. Price 15s.

Spiders: Structure, Landholds and Moves by J. L. CLOUDSLEY-THOMPSON. London: Pergamon Press. 1958. Price 50s.

Laboratory Directions in General Zoology by MARY J. GUTHRIE & J. M. ANDERSON. New York: Wiley; London: Chapman & Hall. 1958. Price 28s.

The Wandering Albatross by WM. JAMESON. London: Hart-Davis. 1958. Price 16s.

Koedoe. Journal for Scientific Research in the National Parks of the Union of South Africa. No. 1. Pretoria. 1958.

Portrait of a Wilderness [The story of the Cape Deforma Expedition] by GUY MOUNTFORT. London: Hutchinson. 1958. Price 30s.

The Badger by ERNEST NEAL. Harmondsworth: Penguin Books. Pelican edition 1958. (Original edition: Collins 1948.) Price 3s. 6d.

Lord's Company by LESLIE KELLY. London: Murray. 1958. Price 25s.

The Wildfowl Trust—Ninth Annual Report [for 1956-57]. Edited by P. SCOTT & H. BOYD. London: Country Life. 1958. Price 10s.

The Ecology of Invasions by Animals and Plants by C. S. ELTON. London: Methuen. 1958. Price 30s.

ABSTRACTS

The abstracts are edited by Professor L. A. Harvey with the assistance in selecting and abstracting of J. A. Allen, J. D. Brayshaw, G. I. Crawford, T. A. W. Davis, A. E. Ellis, F.A.O., Fisheries Division, P. D. Gabbutt, N. A. Holme, D. Leatherdale, A. Macfadyen, C. Matheson, E. J. Moynahan, Miss E. Nelmes, W. R. Pickering, J. L. Cloudsley-Thompson, G. G. Vickers, Mrs M. Vincent, M. Williamson and W. B. Yapp. References are checked by B. M. Hobby. Mr R. S. R. Fitter, with the help of the societies themselves, aims to cover all the proceedings, transactions and journals of local natural history societies and field clubs. Secretaries of such organizations are urged once again to aid this work by making sure that copies of their publications are sent, regularly, to **R. S. R. Fitter, Esq., Drifts, Chinnor Hill, Oxford.** Readers and authors can materially assist by pointing out errors and omissions, and by sending reprints or offers of help in making abstracts to **Professor L. A. Harvey, The University, Exeter.**

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CONTENTS

Note. In order to avoid unnecessary overlap with journals which the ecologist would be likely to consult in any case, papers in the *Journal of Animal Ecology* are not noticed, nor are:

(*a*) papers in *British Birds* which would fall in '4. Food and food habits';

(*b*) papers in the above journal and in *The Entomologist's Record* and *The Entomologist's Monthly Magazine* which would be classified in '5. Migration, introductions and local distribution'.

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1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and Brackish

Bagenal, T. B. 1957. The vertical range of some littoral animals on St. Kilda. *Scot. Nat.* **69**, 50-1.

Ballantine, D. & Abbot, B. C. (1957). Toxic marine flagellates: their occurrence and physiological effects on animals. *J. Gen. Microbiol.* **16**, 274-281.

A brief report on the occurrence of 'red tides' and other blooms and on physiological effects of algal toxins.

Barnes, H. 1957. Processes of restoration and synchronization in marine ecology. The spring diatom increase and the 'spawning' of the common barnacle, *Balanus balanoides* (L.). *Année Biol.* (3), **33**, 67-85.

Importance of synchronization of naupliar release and the vernal diatom outburst.

Barnes, H. 1958. Processes of restoration and synchronization in marine ecology. The spring diatom increase and the 'spawning' of the common barnacle, *Balanus balanoides* (L.). *Un. Int. Sci. Biol.* B **24**, 67-85.

Field and experimental observations on the part played by the stimulus for the release of nauplii by the barnacle in the synchronization of naupliar development with the spring diatom outburst.

Barnes, H. & Barnes, M. (1957). Resistance to desiccation in intertidal barnacles. *Science*, **126**, 358.

Means of reducing water loss shown by intertidal barnacles.

Crisp, D. J. & Patel, B. S. (1958). Relation between breeding and ecdysis in cirripedes. *Nature, Lond.* **181**, 1078.

Experiments in the relation of moulting to copulation and to carriage of embryos. As starved barnacles moult it is thought that ecdysis must have another function other than allowing for growth.

Crisp, D. J. & Southward, A. J. (1958). The distribution of intertidal organisms along the coasts of the English Channel. *J. Mar. Biol. Ass. U.K.* **37**, 157-208.

Distribution of the commoner plants and animals of rocky shores in the English Channel. Observed distribution related mainly to temperature.

Davies, J. L. (1956). The grey seal at the Isles of Scilly. *Proc. Zool. Soc. Lond.* **127**, 161-166.

A study of a small and diminishing colony. Notes are given on breeding behaviour and a short-term marking technique.

Drinnan, R. E. & Cole, H. A. 1957. Oystercatchers (*Haematopus ostralegus*) as pests of cockle and mussel beds. *Nature in Wales*, **3**, 499-503.

Damage by oystercatchers on shellfish-beds may vary considerably from district to district. Large numbers of oystercatchers at the Burry Inlet, South Wales, in winter 1956-57, had very slight effect on the yield of the cockle fishery. At Morecambe Bay, a considerable proportion of the damage to cockles was due to oystercatchers.

Droop, M. R. & Daisley, K. W. (1957). Vitamin B_{12} in marine ecology. *Nature, Lond.* **180**, 1041.

The population level of the chrysomonad, *Monochrysis lutheri*, in pure culture varies with vitamin B^{12} dosage. The suggestion by Droop that vitamin content in the sea has been overestimated in importance, it being always superabundant, is criticized by Daisley.

Durchon, M. (1958). Problèmes posés par le comportement des néréidiens au moment de leur reproduction. *Un. Int. Sci. Biol.* B **24**, 31-42.
Discusses reproductive polymorphism and differences in swarming behaviour among different species of nereid worms.

Gauld, D. T. & Buchanan, J. B. (1956). The fauna of sandy beaches in the Gold Coast. *Oikos*, **7**, 293-301.
Distinguishes steep beaches of coarse sand inhabited only by *Ocypoda hippens* near HWM from flatter beaches of fine sand with richer populations showing zonation like that displayed elsewhere.

Hewer, H. R. (1957). A Hebridean breeding colony of grey seals, *Halichoerus grypus* (Fab.), with comparative notes on the grey seals of Ramsey Island, Pembrokeshire. *Proc. Zool. Soc. Lond.* **128**, 23-66.
Breeding behaviour and vital statistics.

Korringa, P. (1958). Water temperature and breeding throughout the geographical range of *Ostrea edulis*. *Un. Int. Sci. Biol.*, B **24**, 1-17.
A critical review of the evidence and theories on the relation between temperature and spawning in the oyster.

Korringa, P. (1958). On the supposed compulsory relation between oviparous oysters and waters of reduced salinity. *Un. Int. Sci. Biol.* B **24**, 109-116.
Concludes that oviparous oysters are adapted to fluctuating salinity of a low level.

Lewis, J. R. (1957). An introduction to the intertidal ecology of the rocky shores of a Hebridean island. *Oikos*, **8**, 130-160.
A general survey of the fauna and flora of the shores of North Uist, differentiating zonation and effects of shelter and exposure. Loch Maddy, very sheltered, is one of the richest areas known in Britain.

Lewis, J. R. (1957). Intertidal communities of the northern and western coasts of Scotland. *Trans. Roy. Soc. Edinb.* **63**, 185-220.
Describes zonation on rocky shores in these areas.

Marshall, S. M. & Orr, A. P. (1958). The life history of the copepod *Calanus finmarchicus* in different latitudes. *Un. Int. Sci. Biol.* B **24**, 43-47.
Discusses differences in growth, development, migrations and reproduction at different latitudes.

Marshall, S. M. & Orr, A. P. (1958). A preliminary note on seasonal changes in respiration in copepods. *Un. Int. Sci. Biol.* B **24**, 221-226.
Techniques and results of experimental work.

Mason, J. (1957). The age and growth of the scallop, *Pecten maximus* (L.) in Manx waters. *J. Mar. Biol. Ass. U.K.* **36**, 473-492.
Growth rings on the shell of this lamellibranch are laid down annually, in spring, and so can be used to determine age.

Morton, J. E., Boney, A. D. & Corner, E. D. S. (1957). The adaptations of *Lasaea rubra* (Montagu), a small intertidal lamellibranch. *J. Mar. Biol. Ass. U.K.* **36**, 383-405.
A description of the habitat of this inhabitant of rock crevices on the shore, together with experimental data on filtration rates, respiration and resistance to desiccation of individuals living at different levels on the shore.

Newell, G. E. (1958). The behaviour of *Littorina littorea* (L.) under natural conditions and its relation to position on the shore. *J. Mar. Biol. Ass. U.K.* **37**, 229-239.

Newell, G. E. (1958). An experimental analysis of the behaviour of *Littorina littorea* (L.) under natural conditions and in the laboratory. *J. Mar. Biol. Ass. U.K.* **37**, 241-266.
Orientation of winkles in relation to a light-compass reaction and to gravity.

Nordli, E. (1957). Experimental studies on the ecology of Ceratia. *Oikos*. **8**, 200-265.
Details culture of *Ceratium tripos*, *C. fusus*, *C. furca* and *C. lineatum* isolated from samples obtained in Droback Sound, with data on growth-rate, division-rate, optimal salinity, 15-25‰, optimal temperature, 15-20° C. and optimal light intensity, 5000 Lux, *C. tripos*, *C. lineatum*, 2500 Lux, *C. fusus*, *C. furca*, and on cell shape and length. The species are restricted in the Baltic by low salinity, and mass occurrence in the Oslofjord in summer is partly ascribable to favourable temperature and salinity.

Perkins, E. J. (1958). Microbenthos of the shore at Whitstable, Kent. *Nature, Lond.* **181**, 791.
Distribution and abundance of forms that pass through a 1 mm sieve, and collected from sandy flats, with clay subsoil. Seasonal change and sea temperature effects discussed.

Prenant, M. (1958). Zoologie des sables intercotidaux et traduction approximative des données granulométriques en nombres de grains. *C.R. Acad. Sci., Paris*. **10**, 1582-1585.
Estimation of ecological properties of sands by log-log graphic determination of grain number as a function of sieve mesh size.

Qasim, S. Z. (1957). The biology of *Blennius pholis* L. (Teleostei). *Proc. Zool. Soc. Lond.* **128**, 161-208.
Growth studies by means of otoliths and length and weight measurements are combined with examination for sexual condition and egg laying. Growth in length and in weight alternate. Gut analysis shows that most shore invertebrates are eaten.

Rae, K. M. (1957). The plankton around the British Isles. *J. Gen. Microbiol.* **16**, 265-267.
Brief account of plankton species as indicators of water masses, and their relationship to North Sea fisheries.

Shelbourne, J. E. (1957). The feeding and condition of plaice larvae in good and bad plankton patches. *J. Mar. Biol. Ass. U.K.* **36**, 539-552.
Effects of plankton supply on mortality and growth of plaice larvae.

Smith, R. I. (1958). A note on the tolerance of low salinities by nereid polychaetes and its relation to temperature and reproductive habit. *Un. Int. Sci. Biol.* B **24**, 93-107.
Discusses effects of temperature on chloride regulation and of classified salinity regimes on osmoregulation and reproduction.

Southward, A. J. (1958). Note on the temperature tolerances of some intertidal animals in relation to environmental temperatures and geographical distribution. *J. Mar. Biol. Ass. U.K.* **37**, 49-66.
Temperature tolerances of four species of barnacles and four species of top-shells related to their geographical distribution and zonation on the shore. Body temperatures of barnacles and limpets exposed on the shore also measured. Temperatures experienced on shore are well within tolerance limits, these do not therefore have a direct effect on distribution.

Spärck, R. (1958). The importance of metabolism in the distribution of marine animals. *Un. Int. Sci. Biol.* B **24**, 233-239.
Discusses relations between ecological and physiological factors and marine zoogeography.

Staiger, H. (1958). Genetical and morphological variation in *Purpura lapillus* with respect to local and regional differentiation of population groups. *Un. Int. Sci. Biol.* B **24**, 251-258.

Examines genetic heterogeneity and phenotypic polymorphism of the dog-whelk and discusses the value of such littoral species in studying the relation between population genetics and the environment.

Swedmark, M. (1958). Variation de la croissance et de la taille dans différentes populations du téléostéon *Gobius minutus*. *Un. Int. Sci. Biol.* B **24**, 163-170.

Compares populations of this fish in Brittany and in Sweden in terms of varying ecological conditions, chiefly temperature and salinity.

Tucker, D. W. & Newnham, C. T. (1957). The blue shark *Prionace glauca* (L.) breeds in British seas. *Ann. Mag. Nat. Hist.* (12) **10**, 673-688.

The Looe fishery is shown to be based effectively on gravid females of this shark, regarded hitherto as not breeding in British waters.

Venables, U. M. & Venables, L. S. V. (1957). Mating behaviour of the seal *Phoca vitulina* in Shetland. *Proc. Zool. Soc. Lond.* **128**, 387-396.

Detailed descriptions of mating behaviour are given and compared with observations of this and related species from other areas. Population counts and human killings over three years are given.

(*b*) Fresh Water

Baxter, E. W. (1957). Lamprey distribution in streams and rivers. *Nature, Lond.* **180**, 1145.

The building of ammocoete beds is related to the gradient of a river, but once established they will withstand changes in water level and flow, unless they dry out. Lampreys differ in this respect from many other populations inhabiting rivers; and live outside the environment of the main stream.

Corbet, P. S. (1957). The life-histories of two summer species of dragon-fly (Odonata: Coenagriidae). *Proc. Zool. Soc. Lond.* **128**, 403-418.

Two semivoltine species—*Coenagrion mercuriale* and *Ceriagrion tenellum* are discussed. A mechanism for synchronization of emergence is proposed.

Corbet, P. S. (1958). Effects of *Simulium* control on insectivorous fishes. *Nature, Lond.* **181**, 570-571.

Fish react to the removal of aquatic insects by insecticides, by changing diet, by retreating to undisturbed spots or by moving from the district.

Downing, K. M. & Merkens, J. C. (1957). The influence of temperature on the survival of several species of fish in low tensions of dissolved oxygen. *Ann. Appl. Biol.* **45**, 261-267.

The resistance to low oxygen tensions is correlated with temperature gradients for rainbow trout (*Salmo gairdnerii*), perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), mirror carp (*Cyprinus carpio*), tench (*Tinca tinca*), dace (*Leuciscus leuciscus*), chub (*Squalius squalus*) and bleak (*Alburnus alburnus*). Tench were most resistant to lack of oxygen and trout most susceptible.

Lindahl, K. Curry- (1957). The occurrence of the char, *Salmo alpinus*, in running waters in arctic and high boreal areas in Sweden. *Kungl. Fysiogr. Sällk. Lund. Förh.* **27**, 161-172.

Discusses the distribution of the char in relation to *Salmo trutta* and also to latitude and altitude.

Melluish, W. D. (1957). The census of great crested grebes 1946 to 1955. Final report and summary of results. *Lond. Bird Rep.* **21** (1956), 48-57.

Tabulates numbers of birds observed each year of the census at each water surveyed. 627 grebes were present in 1953 falling to 445 in 1955. The average over the ten years was 470, with 239 of gravel pits, 231 on other waters. On average 45% of apparently suitable waters were used each season. Non breeding birds comprised probably 60% of the populations.

Milne, R. G. (1957). A study of the mill races and sluices at Flatford Mill and Dedham. *Trans. Suffolk Nat. Soc.* **10**, 27-38.

Lists the fauna and flora, and discusses the distribution of Cladophora and the food and feeding methods of various animals.

Northcote, T. G. (1958). Effect of photoperiodism on response of juvenile trout to water currents. *Nature, Lond.* **181**, 1283-1284.

Description of apparatus used and the results obtained. Fingerling trout acclimatized to certain temperatures and photoperiods when moved to the current causing apparatus, gave responses varying with the daylengths to which the trout had been subjected. If this had been short the trout tended to move upstream and vice versa. This reaction may be significant in directing movement into lakes.

Reynoldson, T. B. (1957). Population fluctuations in *Urceolaria mitra* (Peritricha) and *Enchytraeus albidus* (Oligochaeta) and their bearing on regulation. *Cold Spring Harbour Sympos. Quant. Biol.* **22**, 313-327.

Compares population regulation by density dependent factor, suitable living space, of *Urceolaria* living under favourable conditions epizoic on freshwater triclads, with absence of such control of other *Enchytraeus*, in sewage bacteria beds, or lumbricids, in wet dunelands. Concludes that such 'fringe' populations may persist by virtue of a 'probability' safety valve in the heterogeneity of their distribution within patchy environmental conditions.

Smyly, W. J. P. (1957). The life-history of the bullhead or miller's thumb (*Cottus gobio* L.). *Proc. Zool. Soc. Lond.*, **128**, 431-453.

A study of life-history, breeding biology, parasites, growth rate and feeding in lake and river of nearly 3000 specimens.

Smyly, W. J. P. (1957). Observations on the life history of the harpacticoid copepod, *Canthocamptus staphylinus* (Jurine). *Ann. Mag. Nat. Hist.* (12), **10**, 509-512.

Records the life-cycle in a Westmorland tarn, with one generation per year and dormant, encysted adults in summer.

(*c*) Land

Adams, L. E. G. (1957). Nest records of the swallow. *Bird Study*, **4**, 28-33.

A Nest Record Card summary in condensed form. Succinct statements of usual data on breeding period, clutch size, incubation and fledging periods and breeding success.

Armstrong, E. A. (1958). Notes on the wren in the Aran Islands, Ireland. *Brit. Birds* **51**, 29-35.

The Aran Islands provide habitats for wrens intermediate between those of the 'fertile' mainland and 'bleak' islands e.g. St. Kilda and Shetland. Observations showed breeding behaviour to conform mainly to the fertile area type with indications of a tendency towards the bleak area type.

Baker, P. F. (1957). Population studies of the common earwig (*Forficularia auricularia* Linn.) at Lincoln. *Trans. Lincs. Nat. Union*, **14**, 94-99.

Males and females were present in almost equal numbers in a Lincoln garden during an earwig plague. When individuals were marked a small daily movement was detected, up to 12 ft from the place of marking, but most were recaught within 3 ft.

Barne, M. E. St. J. (1958). Some notes on the coypu. *Trans. Suffolk Nat. Soc.*, **10** (3), 243.
Brief notes on *Myocastor coypus*, a south American mammal established in East Anglia.

Benson, G. B. G. (1957). Some notes on marsh harriers. *Trans. Suffolk Nat. Soc.* **10,** 62-66.
Notes on breeding biology.

Boyd, J. M. (1957). Comparative aspects of the ecology of Lumbricidae on grazed and ungrazed natural maritime grassland. *Oikos*, **8,** 107-121.
Compares earthworm populations of grazed and ungrazed areas of the airfield on Tiree, trapping in batteries of sunk jam-jars and artificial dung pats. The species patterns differ, and distribution is heterogeneous. Reproduction in ungrazed ground is continuous with sharp mid-winter and spring peaks, but is confined to winter and spring in grazed ground.

Boyd, J. M. (1957). Animals and humans at St. Kilda. *Discovery*, **18,** 344-348.
A summary of the history and ecology of St. Kilda, giving in particular recent counts of Soay and blackface sheep, St. Kilda house-mouse, St. Kilda field mouse, St. Kilda wren and Leach's petrel. Attention is drawn to the future of the area as included in the Air Ministry's guided-missile range.

Brereton, J. Le G. (1957). The distribution of woodland isopods. *Oikos*, **8,** 85-106.
Describes daily and seasonal distribution of four common species of woodlice in mixed hard wood at Wytham, Oxford, during 1953 and 1954; briefly discusses significance of inter species relationships.

Briggs, J. B. (1957). Some features of the biology of the winter moth (*Operophtera brumata* (L.)) on top fruits. *J. Hort. Sci.* **32,** 108-125.
A phenological study of the winter moth from 1951 to 1956. The dormancy of eggs in relation to fruit-bud development, rate of larval development, and larval dispersal in air currents are considered. The seasonal activities of male and female moths are discussed. The first emergence of adults was not related to the incidence of autumn frosts, although subsequent emergence was delayed by low temperatures.

Cadman, W. A. (1957). Vole damage in Wales 1956-57. *Nature in Wales*, **3,** 504-507.
A summary of the effects on nurseries and plantations of the vole population peak during these two years.

Carthy, J. D. (1957). Polarized light and animals. *Discovery*, **18,** 105-109.
An outline of the response of arthropods to polarized light, and of its value in direction-finding by sawflies, ants and bees.

Christensen, B. (1956). Studies on Enchytraeidae 6. Technique for culturing Enchytraeidae, with notes on cocoon types. *Oikos*, **7, 302-307.**
Describes a simple breeding chamber and its manipulation. Two types of cocoon related to different species.

Comfort, A. (1957). Survival curves of mammals in captivity. *Proc. Zool. Soc. Lond.* **128, 349-364.**
Life tables and survival curves are given for eight species and compared with those of wild and domestic species.

Coulson, J. C. & White, E. (1958). The effect of age on the breeding biology of the kittiwake *Rissa tridactyla*. *Ibis*, **100,** 40-51.
Marked kittiwakes were studied over three seasons. Birds which had bred previously returned to the colony earlier than those breeding for the first time, laid more eggs earlier, and had greater breeding success. Breeding birds showed strong colony tenacity; but 24% of marked non-breeders were later seen in other colonies. (See 1956, *Ibis*, **98,** 63-79 and abstract in 1956, *J. Anim. Ecol.* **25,** 441.)

Cox, D. R. & Smith, W. L. (1957). On the distribution of *Tribolium confusum* in a container. *Biometrika*, **44**, 328-335.

The density of beetles is lowest in the centre, increases out to the edges and is highest in the corners. This would be expected if the beetles move in straight lines until they hit an edge and then either return the way they have come or move along the edge a bit before setting off again in a new direction.

Crowcroft, P. (1956). On the life span of the common shrew (*Sorex araneus* L.). *Proc. Zool. Soc. Lond.* **127**, 285-291.

Weights and measurements are given including reproductive condition and canine tooth length (as an index of age) over two years. Shrews do not breed in the year of birth and die by the end of the second autumn.

Dicker, G. H. L. & Tew, R. P. (1957). Some experiments to investigate the control of apple sawfly, *Hoplocampa testudinea* (Klug), by concentrate sprays. *J. Hort. Sci.* **32**, 254-264.

Primarily concerned with control of the apple sawfly, but contains original observations on embryonic and larval development in relation to temperature fluctuations in the field.

Dobson, R. M., Stephenson, J. W. & Lofty, J. R. (1957). Quantitative studies of adult populations of wheat bulb fly, *Leptohylemyia coarctata* (Fall.) in the field. *Ann. Appl. Biol.* **45**, 385-386.

A quantitative study of a natural population of wheat bulb fly at Rothamsted in 1956.

Duffey, E., Locket, G. H. & Millidge, A. F. (1958). The spider fauna of the heaths and fens in West Suffolk. *Suffolk Nat. Trans.* **10** (3), 199-209.

Records from 1955 to 1957 and a special survey of the fens and brecklands in 1956, with descriptions of the ecology of the principal sites. Seventy-one species recorded in fens and marshes, sixty on the Breck. Discusses the significance of some distributions.

Elton, C. (1957). Interspecific competition. *Nature, Lond.* **180**, 1002.

A clarification of the term 'competition' as understood by Elton & Miller (1954).

Gompertz, T. (1957). Some observations on the feral pigeon in London. *Bird Study*, **4**, 2-13.

Surveys feeding, breeding, excretory and roosting habits of 'London' pigeons. They are remarkably similar to those of the Rock Dove as observed on Islay. Discusses influence of man on the birds.

Griffiths, D. J., Holden, J. H. W. & Jones, J. M. (1957). Investigations on resistance of oats to stem eelworm, *Ditylenchus dipsaci* Kühn. *Ann. Appl. Biol.* **45**, 709-720.

New sources of resistance to the stem eelworm revealed by a study of some 250 forms of oats.

Hattingh, I. (1956). Measurements of foxes from Scotland and England. *Proc. Zool. Soc. Lond.* **127**, 191-199.

Data of weights and measurements from 87 foxes and measurements of skull dimensions are used to establish that there are racial differences between Scottish and English, but not between Westmorland and other English foxes.

Hooper, J. H. D. & Hooper, W. M. (1956). Habits and movements of cave-dwelling bats in Devonshire. *Proc. Zool. Soc. Lond.* **127**, 1-26.

A ringing study involving 2040 individuals in six species over six years; 62% recovery was obtained. Interchange of population between three main colonies of greater horseshoe (*Rhinolophus ferrumequinum*) was studied and movements up to forty miles detected. This and other species were studied for hibernation, sex ratio, ectoparasites and weight changes.

Hussey, N. W. (1957). Observations on the Sphaeroceridae (Borboridae, Diptera) associated with stable manure. *Ann. Mag. Nat. Hist.* (12), **10,** 762-766.
Seasonal occurrence of sixteen species reared from stable manure at Littlehampton. A comparison with the population of cow manure is made.

Jackson, R. D. (1958). A study of a population of robins, *Erithacus rubecula*. *Irish Nat. J.* **12,** 229-236.
52 robins were ringed and studied in a Dublin suburban area. The average size of the autumn territory is less than a sixth that of the breeding one, and the maximum number of territories are held in autumn. The population was also studied in the breeding season.

Johnson, C. G., Haine, E., Cockbain, A. J. & Taylor, L. R. (1957). Moulting rhythm in the alienicolae of *Aphis fabae* Scop. (Hemiptera: Aphididae) in the field. *Ann. Appl. Biol.* **45,** 702-708.
A study of the daily fluctuations in moulting rate in a natural population of the bean aphis on field beans, and of probable causative factors.

Johnson, C. G., Taylor, L. R. & Haine, E. (1957). The analysis and reconstruction of diurnal flight curves in alienicolae of *Aphis fabae* Scop. *Ann. Appl. Biol.* **45,** 682-701.
Experimental information derived from marked alatae of the bean aphis was used to construct theoretical daily curves for numbers migrating from a bean crop. Comparison of these with observed curves gave data on the effect of light intensity, temperature, and rate of production of alatae on migrationary behaviour.

Lacey, W. S. (1958). Some effects of myxomatosis on vegetation, with special reference to Ynys Seiriol. *Trans. Anglesey Antiq. Soc. Fld. Cl.* **1957,** 26-33.
Discusses the plants in terms of the feeding-preferences of rabbits, and the results on Puffin Island of the destruction of the rabbit. Comparison with previous flora lists shows the largest number of species yet recorded and a large influx of new species.

Lack, D. (1958). The significance of the colour of turdine eggs. *Ibis,* **100,** 145-166.
Colour is shown to be valueless in classification, but to be associated with the nest-site: eggs in deep holes tend to be immaculate white, and to be progressively more spotted and blotched as the nest is more exposed.

Lack, D., Gibb, J. & Owen, D. F. (1957). Survival in relation to brood-size in tits. *Proc. Zool. Soc. Lond.,* **128,** 313-326.
Nestling weight was usually higher in smaller broods of great and blue tits. Survival was usually maximal from modal size clutches but in years of abundant food modal clutch size and size having maximal survival were higher. Late broods are rare and less successful.

Lack, D. & Lack, E. (1958). The nesting of the long-tailed tit. *Bird Study,* **5,** 1-19.
Six years' observations on the biology of this non-territorial bird in Wytham Wood, Oxford, using colour ringing. Data are compared with B.T.O. records and with the Swedish habits of the bird. Data on nest sites, repeat nests, laying time, clutch size, communal feeding and young and on losses, highest during incubation.

Larson, S. (1957). The suborder Charadrii in arctic and boreal areas during the tertiary and pleistocene. A zoogeographic study. *Acta Vert.* **1,** 1-84.
Traces the evolution of charadrine birds in relation to climatic and ecological changes and discusses taxonomic differentiations in relation to zoogeographic patterns of various kinds.

Laundon, J. R. (n.d.). The bird ecology of a Northamptonshire woodland. *The First Fifty Years,* 114-122.
A study of the birds of an oak-ash wood near Corby.

Long, D. B. (1957). Oviposition of wheat bulb fly, with special reference to crop and site selection. *Ann. Appl. Biol.* **45,** 388.

Infestation levels of wheat bulb fly (*Leptohylemyia coarctata*) considered in relation to previous field cropping.

MacRae, C. (1957). Some observations on *Tortrix* defoliation. *Quart. J. For.* **51,** 332-333.

In an epidemic of *Tortrix viridana* in Lancashire in 1956 the least damaged trees were those which flushed earliest.

Mutchmor, J. A. & Beckel, W. E. (1958). Importance of photoperiodism and temperature in inducing diapause in the european corn-borer, *Pyrausta nubilasis* (Hbn.). *Nature, Lond.* **181,** 204.

Experiments indicate the importance of temperature and photoperiod in the initiation of diapause in relation to changed seasonal habits with a facultative second generation of this moth in Canada.

Nørgaard, E. (1956). Environment and behaviour of *Theridion saxatile*. *Oikos,* **7,** 159-192.

Describes the life cycle, nesting, hibernation, food, family social behaviour and local distribution of this spider. Particular attention to temperature tolerance at all stages, this being investigated experimentally.

O'Connor, F. B. (1957). An ecological study of the enchytraeid worm population of a coniferous forest soil. *Oikos,* **8,** 161-199.

Populations in mor type humus beneath a pure Douglas Fir stand in north Wales ranged from 42,000/m² in winter to 250,000/m² in summer and showed aggregative distribution. Distribution was positively correlated with temperature, moisture only being important in the litter layer. Effects of drought were studied, and the observations contrasted with conditions in Denmark.

Pressland, D. E. (1956). The vertical zonation of butterflies on Reigate Hill, Surrey. *Starfish,* **9,** 22-24.

Zonation of butterflies on a chalk hillside climbing rather steeply from 525 to 763 feet, with some preliminary displacement experiments.

Radford, M. C. (1957). Observations on broods of nuthatches leaving the nest. *Brit. Birds,* **50,** 526-528.

A brood was watched leaving a nest-box in three seasons. In 1953 and 1956 the young were vigorous and the nest was clean, but in 1956 two much less mature fledglings emerged and spent much time preening, and the nest was found to be foul with grubs and insects.

Ratcliffe, D. A. (1958). Broken eggs in peregrine eyries. *Brit. Birds,* **51,** 23-26.

At fourteen of the eyries examined by the writer between 1949 and 1956 one or more eggs were broken. He suggests that the majority of the broken eggs were probably eaten by the peregrines.

Robertson, D. (1957). The wood-pigeon problem. *Scot. Agric.* **36,** 209-211.

Includes information on the winter movement of wood-pigeon flocks in north-east Scotland, based on questionnaire replies from foresters in the area. Flocking starts from the end of October, when the birds move southwards; in the first week of March the northwards journey begins, the flocks then containing about a third of young birds.

Rockstein, M. & Lieberman, H. M. (1958). Survival curves for male and female house-flies (*Musca domestica* L.). *Nature, Lond.* **181,** 787-788.

There is a marked difference in the maximum and average longevities of the two sexes.

Rothschild, M. & Marsh, H. (1956). Increase of hares (*Lepus europeus* Pallas) at Ashton Wold, with a note on the reduction in numbers of the brown rat (*Rattus norvegicus* Berkenhout). *Proc. Zool. Soc. Lond.* **127,** 441-445.

Changes considered to be associated with rabbit myxomatosis, and possibly with local movements. Reduction of rats perhaps due to predation by foxes.

Sandeman, P. W. (1957). The breeding success of golden eagles in the southern Grampians. *Scot. Nat.* **69,** 148-152.

A survey of 14 eagle territories; lower breeding success in some areas was due largely to human interference.

Sankey, J. (1955). Observations on the European badger *Meles meles meles* (L.). *S.E. Nat. Antiq.* **1955,** 20-34.

Notes on habits, food, behaviour, voice, disease and growth rate from captive and wild animals. Describes an old badger pit.

Shanahan, P. (1957). The distribution of the bean gall sawfly *Pontania proxima* (Lep.) (Hym. Tenthredinidae) on *Salix fragilis* L. *Ent. Mon. Mag.* **93,** 182-183.

First brood galls are randomly distributed on trees; second brood galls are concentrated near the tops of trees. Reasons for this are discussed and are criticized in a note added by R. B. Benson.

Sharman, G. A. M. (1958). Liver flukes. *Scot. Agric.* **37,** 203-205.

Brief account of harm done by liver flukes to farm animals. In four months at the end of 1957, 11·5% of cattle livers and 1·0% of sheep livers were condemned at Inverness slaughter house.

Sheals, J. G. (1957). Animal life in soils. *Discovery,* **18,** 514-518.

A brief outline of soil zoology.

Shorten, M. (1957). Damage caused by squirrels in Forestry Commission areas, 1954-56. *Forestry,* **30,** 151-172.

From questionnaires in 1954-5-6 on damage done by *Sciurus carolinensis* and *S. vulgaris leucourus,* mainly the stripping of bark from the stems of growing trees. At a shilling a tail nearly £33,000 was paid in bounties in two and a half years; there are indications that this has led to a decrease in damage.

Smith, D. Summers- (1958). Nest-site selection, pair formation and territory in the house-sparrow *Passer domesticus. Ibis,* **100,** 190-203.

House-sparrows normally pair for life and occupy the same nest-site. Replacement of lost mates takes place from February till the end of the breeding season and in autumn. First year males remaining unpaired take up nest-sites from February onwards, and may attract young females. Nesting is colonial and the nest-site only is defended as territory.

Smith, M. Palmer- (1957). Robins rearing two broods in an unusual 'screened' nest. *Brit. Birds,* **50,** 492.

A nest in the hollow of a pollard chestnut overgrown with *Clematis* had a screen of dead leaves hiding it. It was used for a second brood soon after the first was fledged.

Snow, D. W. (1958). The breeding of the blackbird *Turdus merula* at Oxford. *Ibis,* **100,** 1-30.

A complete breeding record for 59 pairs obtained over four seasons in a garden habitat, with less detailed observations on a woodland population. Yearling females laid smaller clutches than old ones, and averaged fewer broods in the season. Broods were larger on average in woodland, clutches being larger and nestling mortality lower, but the population is less successful owing to heavy predation.

Stokes, B. M. (1957). Laboratory experiments on larval behaviour of wheat bulb fly. *Ann. Appl. Biol.* **45,** 386-387.
In vitro studies of host plant selection by the wheat bulb fly, *Leptohylemyia coarctata*.

Taverner, J. H. (1958). Observations on a corn bunting roost. *Brit. Birds,* **51,** 126.
A Hampshire roost in reeds was occupied in October and November 1956 by up to 80 corn buntings. Brief mention of other corn bunting roosts in reeds is made.

Thompson, J. L. Cloudsley- (1956). Diurnal rhythms in activity of terrestrial arthropods. *Nature, Lond.* **178,** 215.
Suggests that microclimate is the main control of crepuscular activity in insects.

Wallace, H. R. (1957). The stimulatory properties of some organic substances on cysts of the beet eelworm, *Heterodera schachtii* Schmidt. *Ann. Appl. Biol.* **45,** 251-255.
Although no significant differences were found between the rates of larval emergence from beet eelworm cysts in glutamic acid, galactinol, inositol, or water, yet the rate was significantly higher in beet-root diffusata. The importance of root exudates in relation to the eelworm is discussed.

Wallace, H. R. (1958). Movement of eelworms. I. The influence of pore size and moisture content of the soil on the migration of larvae of the beet eelworm, *Heterodera schachtii* Schmidt. *Ann. Appl. Biol.* **46,** 74-85.
Experiments on the effects of soil particle size, pressure deficiencies, and water-film thickness supplies most of the information required about the physical properties of the soil in relation to eelworm movement.

Wallace, H. R. (1958). Movement of eelworms. II. A comparative study of the movement in soil of *Heterodera schachtii* Schmidt and of *Ditylenchus dipsaci* (Kühn) Filipjev. *Ann. Appl. Biol.* **46,** 86-94.
Optimum soil particle size for the movement of the beet eelworm (*H. schachtii*) and the stem eelworm (*D. dipsaci*) was 150-250 and 250-500 μ respectively. A relationship was established between the form of the body waves and the speed of the eelworms; a relationship is also suggested between body length, particle size and speed.

Ward, M. D. (1956). The feeding ecology of the common redstart. *Starfish,* **9,** 13-17.
Redstarts were studied in Hainault Forest, Essex. At certain times there was a considerable difference in the feeding habits of the cock and hen birds.

Watson, A. (1957). The breeding success of golden eagles in the north-east Highlands. *Scot. Nat.* **69,** 153-169.
A survey of 12-14 eagle territories; away from one deer forest the density was lower, mainly because of human persecution.

Widdowson, E. & Wiltshire, G. H. (1958). The potato-eelworm hatching factor. *Ann. Appl. Biol.* **46,** 95-101.
A comparison of the properties and biological activities of the eelworm hatching factor from potato root diffusate and eclepic acid from tomato roots and *Solanum nigrum*. Both materials showed maximum hatching activity at about 0·1 mg/l.

2. METHODS, APPARATUS, POPULATION STATISTICS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Bailey, N. T. J. (1956). On estimating the latent and infectious periods of measles. II. Families with three or more susceptibles. *Biometrika,* **43,** 322-331.
Theory and an example.

Bailey, N. T. J. (1956). Significance tests for a variable chance of infection in chain-binomial theory. *Biometrika,* **43,** 332-336.
A test for the assumption that the chance of infection is constant.

Bartlett, M. S. (1957). On theoretical models for competitive and predatory biological systems. *Biometrika,* **44,** 27-42.
Simple stochastic extensions of the logistic curve and of the Lotka-Volterra predator-prey and competition systems. Graphs of artificial realizations of these extensions are given. Stochastic variation and time lags seem to account for some of the phenomena found by Gause. It is stressed that the total size of each replicate population should be given when reporting laboratory experiments.

Boratyński, K. (1957). On the two species of the genus *Carulaspis* Macgillivray (Homoptera: Coccoidea, Diaspidini) in Britain. *Ent. Mon. Mag.* **93,** 246-251.
A key is given to the two species of *Carulaspis* recorded from Britain, with descriptions of the two species and notes on their biology.

Brindle, A. (1957). The ecological significance of the anal papillae of *Tipula* larvae (Dipt., Tipulidae). *Ent. Mon. Mag.* **93,** 202-204.
Forty-five British species of *Tipula* larvae are separated into six groups according to the length of the anal papillae, and it is pointed out that, in general, the size and number of the papillae increase with the degree of wetness of the habitat.

Brindle, A. B. (1957). Notes on the biology of north-east Lancashire Brachycera (Diptera). *Ent. Rec.* **69,** 161-167, 188-192.
Includes a key to the larvae (excluding the Phoridae), with notes on the distribution, flight period, possible habitats and food of a number of species in north-east Lancashire.

DeLury, D. B. (1958). The estimation of population size by a marking and recapture procedure. *J. Fish. Res. Bd. Canada,* **15** (1), 19-25.
Compares Schumaker and Schnabel estimates and prefers latter formula which is extended to cover mortality and recruitment in the population.

Gilbert, N. E. G. (1956). Likelihood function for capture-recapture samples. *Biometrika,* **43,** 488-489.
A modified binomial function for use with chains of samples. This function is almost as accurate as the hypergeometric function and is easier to use.

Graham, M. W. R. de V. (1957). A revision of the Walker types of Pteromalidae (Hym., Chalcidoidea). Part 3 (including descriptions of new species). *Ent. Mon. Mag.* **93,** 217-236.
A revision of the taxonomy of collected material of chalcid wasps is given, with descriptions of new species.

Jewell, G. R. (1956). Marking of tsetse flies for their detection at night. *Nature, Lond.* **178,** 750.
Uses B.T.H. 'Dayglo' powders in solution, painted on the thorax. Detection by ultra-violet light.

Leslie, P. H. (1957). An analysis of the data for some experiments carried out by Gause with populations of the protozoa, *Paramecium aurelia* and *Paramecium caudatum. Biometrika,* **44,** 314-327.
The logistic equation fits the growth curve of both species satisfactorily. The assumption that each species affects the density of the other in the same way that it affects its own leads to a successful prediction of the results of the competition experiments.

Lumsden, W. H. R. (1958). A trap for insects biting small vertebrates. *Nature, Lond.* **181,** 819-820.
Description of construction and some indications of efficiency of a trap suitable for small flying insects.

Nicholson, E. M. (1958). Telescopes and binoculars: some recent improvements in design and their value for bird-watching. *Brit. Birds,* **51,** 133-139.
New types of telescopes lighter and more compact than traditional models, and a unipod for use where a tripod is inconvenient, are described.

Norris, K. R. (1957). A method of marking Calliphoridae (Diptera) during emergence from the puparium. *Nature, Lond.* **180,** 1002.
Flies with the head dusted with fluorescent powder are readily identified under ultraviolet light.

O'Rourke, J. & Makings, P. (1958). An inexpensive easily constructed fish-marking tag. *Nature, Lond.* **181,** 577.
Details of construction and attachment given.

Scudder, G. G. E. (1957). The systematic position of *Pachymerus distinguendus* Flor., with a revised key to the British species of *Peritrechus* (Hem., Lygaeidae). *Ent. Mon. Mag.* **93,** 244-245.
Pachymerus distinguendus Flor. is transferred to the genus *Peritrechus* and a key to the British species of this latter genus is given.

Steel, O. W. (1957). Notes on the Omaliinae (Col., Staphylinidae). *Ent. Mon. Mag.* **93,** 157-164.
The rove-beetle genus *Acrolocha* Thomson is described, and a key is given to the six known species, of which one from North America is new to science.

Woodroffe, G. E. (1957). A preliminary revision of the British *Psallus* Fieber (Hem. Miridae), with a description of a new species. *Ent. Mon. Mag.* **93,** 258-271.
Includes a comparative discussion of the aedeagi of the British species of *Psallus* and a key. *Psallus masseei* sp.n., is described.

3. PARASITES

Johnson, B. (1958). Influence of parasitization on form determination in aphids. *Nature, Lond.* **181,** 205-206.
Adults of *Aphis craccivora* fed on mature leaves produced largely alatiform nymphs, whilst those fed on the leaves of seedlings produced apteriform nymphs. Suppression of alatiform characters by the braconid *Lysiphlebus testaceipes* varies directly with the age of nymph infected.

Lapage, G. (1957). Fitness for parasitic life. *Discovery,* **18,** 465-471.
An introductory essay on physiological and morphological adaptation to parasitism.

Nelson, W. A. (1956). Mortality in the sheep ked, *Melophagus ovinus* (L.) caused by *Trypanosoma melophagium* Flu. *Nature, Lond.* **178,** 750.
Masses of crithridia block the posterior midgut and kill the flies.

Nelson, W. A. (1958). Transfer of sheep keds, *Melophagus ovinus* (L.) from ewes to their lambs. *Nature, Lond.* **181,** 56-57.
Contrary to earlier statements it was found that only newly emerged keds passed from ewes to lambs. The older keds die off as a result of *Trypanosoma* infections. Figures given.

Prudhoe, S. (1957). Note on a tapeworm from a yellow-necked field-mouse. *Trans. Suffolk Nat. Soc.* **10,** 66-67.
Catenotaenia lobata from *Apodemus flavicollis.*

Stansfield, G. (1957). The fleas of Skokholm Island. *Ent. Mon. Mag.* **93,** 196-201.
A list of fleas found on birds and in recently deserted nests is given, together with some general observations.

Thompson, G. B. (1957). The parasites of British birds and mammals. XXX. Mallophaga on birds' eggs. *Ent. Mon. Mag.* **93,** 189-190.

Thompson, G. B. (1957). The parasites of British birds and mammals. XXXI. Summary of the records of ticks of sea-birds. *Ent. Mon. Mag.* **93,** 213-216.
A summary of records of four species of ticks found on sea-birds in Britain is given.

4. FOOD AND FOOD HABITS

Chang, J. T. & Wang, M. Y. (1958). Nutritional requirements of the common house fly, *Musca domestica vicina* Macq. *Nature, Lond.* **181,** 566.

Durrant, K. C. (1958). Insect visitors to orchids. *Trans. Norf. Norw. Nat. Soc.* **18** (7), 6-7.
Hymenoptera, Lepidoptera and Diptera visiting *Epipactis palustris* in Norfolk.

Goodman, G. T. (1957). Larva of *Elachista kilmunella* Staint. (Lep., Elachistidae) feeding on *Eriophorum vaginatum* L. *Ent. Mon. Mag.* **93,** 240.
A larva of the moth *Elachista kilmunella* is recorded as feeding on the leaf of cotton-grass.

Lane, C. (1957). Feeding habits of green larvae of *Deilephila porcellus* (L.) (Lep. Sphingidae). *Ent Mon. Mag.* **93,** 257.
Larvae of the small elephant hawk moth are recorded as feeding on bedstraw.

Leatherdale, D. (1957). *Pteronidea salicis* (L.) (Hym., Tenthredinidae) as a garden pest. *Ent. Mon. Mag.* **93,** 257.
Larvae of the sawfly *Pteronidea salicis* are recorded as feeding on an ornamental willow.

Parmenter, L. (1956). On *Syritta pipiens* L. (Syrphidae) and its habits. *Ent. Rec.* **68,** 211-214.
Includes a list of plants visited by this Syrphid. Most have yellow or white flowers.

5. MIGRATION, INTRODUCTIONS AND LOCAL DISTRIBUTION

Allen, A. A. (1956). The Coleoptera of a suburban garden. 5 -Clavicornia (Part 2). *Ent. Rec.* **68,** 215-222.
Notes on the habitats and abundance of a further 75 species. (*See* 1953, *Ent. Rec.* **65,** 225-231 and abstract in 1954, *J. Anim. Ecol.* **23,** 201.)

Allen, A. A. (1957). Unusual indoor winter activity in an *Adalia bipunctata* L. (Col., Coccinellidae). *Ent. Mon. Mag.* **93,** 168.
A ladybird is recorded as flying indoors in January.

Ashe, G. H. (**1957**). *Acrotona nondescripta* (Col., Staphylinidae), a species new to science and to Britain. *Ent. Mon. Mag.* **93,** 252.

It is considered that a rove beetle described as *Atheta* (*Dimetrota*) *sparre-scneideri* Thos. Munst., is in fact new to science and Britain, and the name *Acrotona nondescripta* is proposed.

Barnes, H. (**1957**). The northern limits of *Balanus balanoides* (L.). *Oikos,* **8,** 1-15.

Baynes, E. S. A. (**1958**). Report on migrant insects in Ireland for 1957. *Irish Nat. J.* **12,** 253-255.

1957 was a poor year, only Lepidoptera being certainly reported.

Beard, D. M. (**1957**). Occurrence of *Elminius modestus* Darwin in Ireland. *Nature, Lond.* **180,** 1145.

Several small specimens, the first recorded, in sheltered localities in south-west Cork.

Blackmore, M. (**1956**). An occurrence of the mouse-eared bat *Myotis myotis* (Borkhausen) in England. *Proc. Zool. Soc. Lond.* **127,** 201-203.

Blower, J. G. (**1957**). Some new and little-known British millipedes. *Ann. Mag. Nat. Hist.* (12) **10,** 497-508.

Burton, J. F. (**1957**). Census of heronries, 1954; additions and corrections. *Bird Study,* **4,** 50-52.

Catchpole, I. M. (**1956**). A country diary from Oswestry, 1947. *Trans. Caradoc Fld. Clb.* **13,** 73-80.

Notes mainly on birds and insects seen near Oswestry during the calendar year 1947.

Cawthra, E. M. (**1957**). Notes on the biology of a number of weevils (Col., Curculionidae, occurring in Scotland. *Ent. Mon. Mag.* **93,** 204-207.

Information is given on dates of occurrence, habits, and egg laying for 13 species of weevils.

Cawthra, E. M. (**1957**). A note on the biology of *Gymnetron antirrhini* Payk. (Col. Curculionidae). *Ent. Mon. Mag.* **93,** 251.

Late pupation of the weevil *Gymnetron antirrhini* is recorded.

Collingwood, C. A. (**1958**). Notes on Coleoptera in the Midlands. *Ent. Rec.* **70,** 4-6.

A number of presumedly new county records, including some for species associated with ants. (*See also* 1957, *Ent. Rec.* **69,** 9-14 and abstract in 1957, *J. Anim. Ecol.* **26,** 508.)

Cramp, S. (**1957**). The census of mute swans, 1955 and 1956. *Lond. Bird Rep.* **21** (1956), 58-62.

BTO census revealed 173 nests within twenty miles of St. Paul's in 1955, 188 in 1956, the average density of about 1·5 nests per ten square miles being much higher than the national figure. Nests, most numerous in Middlesex, are mapped, being most frequent along rivers, on park lakes and ponds and in gravel pits. Non-breeding birds were numerous. Average clutch 4·4, of young hatched, 4, and reared 2·4.

Creutzberg, F. (**1958**). Use of tidal streams by migrating elvers (*Anguilla vulgaris* Turt.). *Nature, Lond.* **181,** 857-858.

Catches suggest that elvers are at the surface at flood tides, and on or near the bottom at ebb tides. Discrepancies between these observations and those of Deelder are discussed and explained on the grounds of a temporary halt in migration in front of freshwater outlets.

Crooke, M. & Bevan, D. (1957). Note on the first British occurrence of *Ips cembrae* Heer (Col., Scolytidae). *Forestry*, **30**, 21-28.

During 1955 the larch bark beetle was discovered in 29 localities in Moray, Nairn, Banff and Inverness, the first British records for this species. Probably entered the country in post-war shipments of German timber and persisted in small numbers until damage done to woodlands by the 1953 gale permitted its increase. A conspicuous feature is the twig tunnelling of the adult beetles. In one locality bred in and killed standing European larch some 45 years old.

Dales, R. P. (1957). Pelagic polychaetes from the Bay of Biscay. *Ann. Mag. Nat. Hist.* (12), **10**, 661-664.

A list with estimates of relative abundance derived from hauls made by the 'Sarsia' over three years.

Duffey, E. (1958). *Dolomedes plantarius* Clerck, a spider new to Britain, found in the upper Waveney valley. *Trans. Norf. Norw. Nat. Soc.* **18** (7), 1-5.

A single specimen of this spider taken in Redgrave Fen, with description of habitat and comparison with its British congener.

Edwards, T. G. & Wakely, S. (1958). *Laspeyresia lobarzewskii* Nowicki (*prunivorana* Ragonot). *Ent. Rec.* **70**, 70-71.

This record of a male taken at light in Kent in June 1957 is stated to be the first for Britain (*but see* 1958, *Ent. Rec.* **70**, 71-73 and Huggins, below.

Godfrey, G. K. (1957). Observations on the movements of moles (*Talpa europaea* L.) after weaning. *Proc. Zool. Soc. Lond.* **128**, 287-295.

The range of young moles was followed by the radioactive ring technique.

Guild, W. J. McL. (1957). Occurrence of populations of *Allolobophora limicola* (Lumbricidae) in S.W. Scotland. *Ann. Mag. Nat. Hist.* (12), **10**, 665-668.

First recorded in Britain in 1953, this earthworm occurs in some numbers in the Forest of Ae, Dumfriesshire. Relative abundance in different soils is estimated.

Hale, P. A. (1958). Roach, *Rutilus rutilus* L., occurring in Co. Tyrone. *Irish Nat. J.* **12**, 259-260.

A second locality for this fish, which is an alien in Ireland. It was apparently introduced to provide food for pike and has established itself in the Fairywater River.

Hedley, R. H. & Underwood, C. M. (1957). Living Foraminifera and empty shells from the north Kent coast. *Ann. Mag. Nat. Hist.* (12) **10**, 721-732.

Thirty-eight species from ten stations off Whitstable and Reculver, including one new to Britain. Sixteen were found living offshore, the remainder as dead tests only.

Homes, R. C. (1957). Wildfowl and wader movements in the London Area in the severe weather of February 1956. *Lond. Bird Rep.* **21**, 41-47.

During the exceptionally severe winter of early 1956 there was a great influx of wildfowl and waders into the London Area, some species appearing in unprecedented numbers. There was some evidence that some of the ducks came from the Continent.

Hope, D. F. (1956). The birds of a border mere. *Trans. Caradoc Fld. Cl.* **13**, 97-105.

An ecological record of the varied bird life at Aqualate Mere on the west border of Staffordshire.

Huggins, H. C. (1958). A further record of *Laspeyresia lobarzewskii* Nowicki in Kent. *Ent. Rec.* **70**, 71-73.

Specimens of this moth, misidentified as *L. woeheriana*, were collected in June 1922 in Kent, where they were emerging from wicker baskets, used for harvesting plums, in store in a closed shed.

Ingram, G. C. S. & Salmon, H. M. (1958). The birds of Brecknock. *Brycheiniog* (*J. Brecknock Soc.*), **3**, 182-255.
A historical and topographical introduction is followed by an annotated list of 207 birds recorded in the county.

Johnson, L. C. (1958). Some preliminary observations on the Lenwade pits. *Trans. Norf. Norw. Nat. Soc.* **18** (7), 26-29.
Freshwater fauna of a chain of flooded pits in Norfolk.

Jones, C. Burdon- (1956). Observations on the enteropneust, *Protoglossus koehleri* (Caullery & Mesnil). *Proc. Zool. Soc. Lond.* **127**, 35-58.
Occurs on the shore of Holy Island. A mainly anatomical study with notes on associated fauna and breeding season.

Kirkegaard, J. B. (1958). Records of the Pogonophora in the Skagerrak. *Nature, Lond.* **181**, 1086.
Records of *Siboglinum ekmani* from the deep cold water.

Kyle, D. (1958). Dragonflies in Breconshire, 1957. *Nature in Wales*, **4**, 547-548.
Nine species recorded, of which four are new county records.

Lloyd, L. C. (1956). Recorder's report on vertebrate zoology, 1947-50. *Trans. Caradoc Fld. Cl.* **13**, 52-60.
Gives notes on 83 species of birds recorded during these four years, including various rarities, such as black-throated diver, black-necked grebe, ferruginous duck, little auk and wryneck, with reference to the unusual inland passage of terns in the spring of 1948 and the waxwing invasion of 1947.

Locket, G. H. & Millidge, A. F. (1957). On new and rare British Spiders. *Ann. Mag. Nat. Hist.* (12) **10**, 481-492.

Lockley, R. M. (1958). Seal Marking, 1957. *Nature in Wales*, **4**, 537-543.
One hundred and sixty Grey Seals were ringed by the West Wales Field Society during the year 1957. Three recaptures born on Ramsey Island were found on the coast of Brittany. Speed of travel, winter distribution of young seals, and other matters are discussed.

MacDonald, R. (1957). The Crustacea, Decapoda, of Belfast Lough. *Ann. Mag. Nat. Hist.* (12) **10**, 656-660.

Matheson, C. (1956). Gamebook records of pheasants and partridges in Wales. *Nat. Lib. Wales J.* **9**, 287-294.
Illustrates by figures from Welsh estate gamebooks the great increase of the pheasant during the nineteenth century, and also compares fluctuations in the partridge bags on different Welsh estates over a long period.

Matheson, C. (1957). Further partridge records from Wales. *Brit. Birds*, **50**, 534-536.
Gamebooks from 1866 to 1950 for two estates in Montgomeryshire and Denbighshire are compared. There is considerable correspondence in the fluctuations, and both show a prolonged decrease compared with former times. (*See* 1956, *Brit. Birds*, **49**, 112-114 and abstract in 1956, *J. Anim. Ecol.* **25**, 444).

Matheson, C. (1957). Pheasant and hare records from Welsh gamebooks. *Nat. Lib. Wales J.* **10**, 205-214.
Discusses the history of the pheasant in Wales, and the long-term variations in the brown hare population in Anglesey and Montgomeryshire.

Miles, P. M. (1957). Immigrant Lepidoptera observed in Wales during 1954 and 1955. *Ent. Mon. Mag.* **93,** 184-187.
Lists twelve migrant species of Lepidoptera, including *Phytometra biloba*, new to Britain, two Odonata and a coccinellid beetle, with notes of weather.

Naylor, E. (1957). The occurrence of *Idotea metallica* Bosc. in British waters. *J. Mar. Biol. Ass. U.K.* **36,** 599-602.
Specimens of this isopod crustacean probably reach Britain from the east coast of N. America amongst floating debris carried by the North Atlantic Drift.

Naylor, E. (1957). *Brachynotus sexdentatus* (Risso), a grapsoid crab new to Britain. *Ann. Mag. Nat. Hist.* (12) **10,** 521-523.
Description, with notes on habitat, of this Mediterranean crab now established in Swansea docks.

Niblett, M. (1956). The genus *Ceriocera* Rdi. (Trypetidae). *Ent. Rec.* **68,** 214-15.
Notes on the distribution and bionomics of *C. cornuta* and *C. microcerus*, two little known species that attack *Centaurea scabiosa*.

Peake, J. F. (1958). *Clubiona similis* L. Koch: a spider new to Britain. *Trans. Norf. Norw. Nat. Soc.* **18** (7), 30-32.
Found on dunes at Blakeney Point, Norfolk, in 1956.

Pendlebury, W. J. 1956). Recorder's reports on entomology, 1947-50. *Trans. Caradoc Fld. Cl.* **13,** 61-63.
Mainly notes on Lepidoptera, with a list of ten species of Lepidoptera, six of Coleoptera, two of Hymenoptera and one of Orthoptera, not previously recorded for the area.

Pugh C. H. W. (1957). Sciomyzidae taken in Shropshire and North Wales, except as otherwise stated. *Ent. Rec.* **69,** 212-213.
A list of thirty species, one possibly new to Britain, with habitats and numbers.

Reynoldson T. B. (1956). An Anglesey record of the medicinal leech. *Trans. Anglesey Antiq. Soc. Fld. Cl.* **1956,** 54.
Among over 300 horse leeches collected at Beaumaris reservoir since 1945, a single medicinal leech was found in 1956, gorged with blood showing nucleated corpuscles similar to those of frog.

Richards K. S. (1958). Occurrence of a 'rare' earthworm in Montgomeryshire. *Nature, Lond.* **181,** 575.
Eisenia veneta var. *zebra* in large numbers at Caersws.

Richards, K. S. (1958). Notes on earthworms collected in Montgomeryshire during autumn 1957. *Nature in Wales,* **4,** 544-546.
Eighteen species and subspecies of Lumbricidae collected around Caersws, Montgomeryshire in autumn 1957, including several not previously recorded for the county.

Roots, B. I. (1957). A further contribution to our knowledge of Friend's Lumbricidae. *Proc. Zool. Soc. Lond.* **128,** 119-131.
Additional corrections and confirmations to those covered by Cernosvitov, C. L., 1942, *Proc. Zool. Soc. Lond.* **111,** 237-280.

Ruttledge, R. F. & Watt, R. H. (1958). The distribution and status of wild geese in Ireland. *Bird Study,* **5,** 22-33.
Maps, with estimated numbers, distribution in Ireland during 1946-56 of grey lag, pink-footed, bean, whitefronted, snow, brent and barnacle geese. Discusses potential effects of exploitation of the bogs upon the birds.

Sage, B. L. (1957). Notes on some Coleoptera from Wales. *Ent. Rec.* **69,** 266-267.
A list of eleven species, with habitats and localities, including three new records each for Cardiganshire and Pembrokeshire.

Sage, B. L. (1958). Notes on dragonflies in Wales in 1957. *Nature in Wales,* **5,** 549-551.
Notes on dragonflies from Pembrokeshire, Merionethshire, Cardiganshire and Skomer Island.

Southwood, T. R. E. & Leston, D. (1957). Notes on the nomenclature and zonal occurrence of the *Orthotylus* species (Hem., Miridae) of British salt marshes. *Ent. Mon. Mag.* **93,** 166-168.
Three species of the bug *Orthotylus* are recorded from salt marshes in five localities.

Stroyan, H. L. G. (1956). More Merioneth Aphid records. *Entomologist,* **89,** 302-303
A list of 20 species from the Cader Idris range and Barmouth district, including nine additions to a recent list. (*See* Eastop 1956, *Entomologist,* **89,** 101-103 and abstract in 1957, *J. Anim. Ecol.* **26,** 232.)

6. STUDIES ON BEHAVIOUR

Boyd, A. W. & Nicholson, E. M. (1958). Mating display of snipe. *Brit. Birds,* **51,** 79-80.
Display of an isolated pair culminating in coition was watched for about half an hour. The preliminaries differed from previous descriptions.

Bunn, D. S. (1957). Colour changes in *Araneus quadratus* Clerck (Araneae, Argiopidae). *Ent. Mon. Mag.* **93,** 201.
Two adult female spiders are recorded as changing their colour in captivity, so that they resembled the background.

Goodwin, D. (1958). Further notes on pairing and submissive behaviour of the red-legged partridge *Alectoris rufa*. *Ibis,* **100,** 59-66.
The pairing behaviour of individual captive birds is described. Mutual fear and hostility seem to be necessary since birds that know one another and are at ease together do not pair. (*See* 1953, *Ibis,* **95,** 581-614 and abstract in 1956, *J. Anim. Ecol.* **25,** 207.)

Jones, C. Burdon- & Charles, G. H. (1958). Light reactions of littoral gastropods. *Nature, Lond.* **181,** 129-131.
Experiments testing the reactions of *Littorina littoralis* with plane polarized light, proving that the mollusc orientates itself along the plane of polarized light coming from above.

King, B. (1958). Willow warbler's unusual song and display-flight. *Brit. Birds,* **51,** 83.
Normal song was uttered from a perch, but in the display-flight the bird circled round slowly uttering unusual notes, and returned to the same perch. The song-flight was repeated at least six times.

Luton, W. G. (1957). Display and posturing of the cuckoo. *Brit. Birds,* **50,** 538.
A male displayed without calling to one of two female cuckoos, slowly rotating its tail. It then picked up a leaf, flew away, returned to the other female and exactly repeated the display.

Tinbergen, N. (1957). The functions of territory. *Bird Study,* **4,** 14-27.
Territory results from (i) site attachment, (ii) hostility to other animals, both phenomena having survival value. Intraspecific hostility is one among other dispersion mechanisms and is highly efficient. New analytical approaches are suggested.

Townsend, A. D. (1957). Green sandpiper uttering call of wood sandpiper. *Brit. Birds,* **50,** 537-538.
On two occasions a green sandpiper when flushed with others in August uttered the note of a wood sandpiper. (*See also* King, J. M. B., 1957, *Brit. Birds,* **50,** 168 and abstract in 1958, *J. Anim. Ecol.* **27,** 189.

Venables, L. S. V. & Venables, U. M. (1958). The song-period of the woodpigeon in Flintshire. *Brit. Birds*, **51**, 160-161.

After four years' residence in Flintshire the writers find the song-period of the woodpigeon to be shorter than the accepted period for central England. It is not regular before late March, the volume is large only from the latter half of June to mid-August, and it ceases during the first half of October.

Wallace, D. I. M. (1958). Ruffs displaying in a wintering area. *Brit. Birds*, **51**, 81-82.

Twenty ruffs and two reeves were present at Cambridge Sewage Farm in early February with other waders. None showed any sign of a ruff, but the displays were much like the 'joustings' of breeding birds.

7. REPORTS OF ORGANIZATIONS

Cambridge Bird Club (1957). 30th Annual Report, **1956.**

In addition to the usual classified notes, contains notes on autumn bird migration in the Wash and Lynn Well Lightship.

Derbyshire Ornithological Society (1957). Report for 1956. 29 pp.

Systematic list, arrival and departure of migrants, and summary of numbers of waders seen at Egginton sewage farm on spring and autumn passage.

Devon Bird-watching and Preservation Society (1957). Twenty-ninth Report, **1956** 84 pp.

Systematic list, with supplementary notes for West Somerset; reports on the black redstart and spotted flycatcher inquiries and on the wildfowl counts.

Eggeling, W. J. (1957). Isle of May Bird Observatory and Field Station report for 1956. *Scot. Nat.* **69**, 129-144.

Notes on bird migration, bird breeding populations and myxomatosis, with a list of ringed birds recovered.

Essex Bird Watching and Preservation Society (1958). The Essex Bird Report **1957.**

In addition to the systematic list, contains reports from the four ringing stations and bird observatories in the county, and the results of wildfowl counts at two reservoirs and on the coast.

Kettering and District Naturalists' Society and Field Club (n.d.). The First Fifty Years. 134 pp.

A history of the Society's activities from 1905 to 1955, including also reports on insect life in Northamptonshire, the galls of the county, and the bird ecology of an oak-ash wood.

Oundle School Natural History Society (1957). Annual Report, **1956.** 38 pp.

Faunistic notes on vertebrates, Lepidoptera and their parasites, Rotifera, Cladocera, Mollusca and Turbellaria, with a useful summary of bird nest mortality in the Nene valley near Oundle in 1956 and notes on the wildfowl counts for the area.

Reading Naturalist, No. **8,** 1956.

Contains annual reports on the entomology and ornithology of the district, and notes on the life of the badger by B. J. Thompson.

Ruislip and District Natural History Society (1956). Journal. No. **5,** 32 pp.

Contributions on the Poor's Field Survey; the Colne Valley Wildfowl Survey; annual reports on the mammals and birds of the district; special reports on the great crested and little grebes and mute swan; and summaries of the status of the snakes and of the Lepidoptera (Part IV).

BRITISH ECOLOGICAL SOCIETY

WINTER AND ANNUAL GENERAL MEETING

3 AND 4 JANUARY 1958

Well over 100 members assembled at Queen Mary College for the 1958 Winter Meeting, which commenced at 2.15 p.m. on Friday, 3 January. Eight papers were delivered and discussed, each concerned with some aspect of the ecological significance of pH, base status and related factors. During the Friday afternoon, attention was directed to the activity and distribution of soil organisms in relation to these influences. Dr O. J. W. Gilbert spoke first on the decomposition of leaf litter under different woodland conditions, describing how freshly fallen leaves of birch, lime and oak (contained in nylon hair-nets) were placed in three adjacent but contrasting sites: a mull, a moder-type mor and an acid peat. After six months the nets were collected and their contents analysed. Birch and lime litter disappeared much more quickly from the nets on the mull than from those on the 'acid' sites; this was due to the large litter-feeding invertebrates present on the mull removing whole leaves. However, the estimated loss in dry weight of the leaves remaining within the nets was remarkably similar on all three sites. Oak litter disappeared to the same extent (per leaf and per net) on all three sites.

A more detailed study of oak litter contained in nylon nets and placed on two adjacent but contrasting sites, a mull and a moder, showed no differentiation between sites after eleven months. Ash litter, however, showed a differentiation between sites both on a per net and a per leaf basis, the rates of disappearance being greater on mull. The nitrogen content per unit dry weight of the ash litter on moder, and oak litter on mull and moder, rose with time; whereas that of ash on mull did not change appreciably during the first six months, after which time insufficient material remained for analysis. The absolute quantity of nitrogen per ash leaf on mull showed a decline paralleling the loss in dry matter per leaf; on moder the loss proceeded more slowly than the dry weight loss. This difference between sites may reflect a difference in the mode of attack by heterotrophic organisms, the loss on mull being due mainly to removal of particles of litter by large invertebrates, and on moder mainly to solution or gaseous evolution of material rich in carbon but poor in nitrogen.

Changes in quality of the nitrogenous matter in hazel litter on passage through the gut of *Glomeris*, a typical mull millepede, have been investigated in the laboratory. The fraction of nitrogenous matter soluble in water (ammonia-N—amino-N) is several times greater in the faeces than in the food.

Discussion on this paper, in which G. C. Varley, H. C. Gilson, E. Gorham, E. D. Le Cren and T. B. Reynoldson took part, was concerned chiefly with the mode of action of earthworms in removing leaves, and the reasons for the differences in rate of disappearance of leaves of the several species. In Dr Gilbert's view these were determined chiefly by toughness, size and 'palatability' of leaves.

Dr J. E. Satchell's paper, entitled 'An analysis of soil fauna communities in relation to soil pH', described a survey of the soil and litter fauna of various types of woodland in the south Lake District in the autumn of 1953. Collections were made by searching, pitfall trapping, refuge trapping, Tullgren funnel extraction and by hand sorting litter and soil samples from 36 sites which included oak, birch, hazel, sycamore, pine, spruce and larch woods.

Four hundred and forty-three species of invertebrates were identified from the collections. About one-quarter of them were classified in two associations, a 'mull' fauna association of species limited to or preponderating in soils of pH 5·0 or above, and an 'acid' fauna association of soils of pH 4·2 or below. A statistical method was referred to by which the allocation of any species to one of the associations could be tested against the null hypothesis of its distribution being random.

Lack of evidence of interspecific relationships precluded the description of the associations as communities, but the reasons why the distributions of some of the component species of the associations might coincide were discussed. Special consideration was given to the relationship of the distribution of earthworms to soil pH and the absence of certain species of earthworms from very acid soils was tentatively attributed to the taste of the soil as determined by its hydrogen ion concentration.

During the discussion, T. B. Reynoldson referred to results of experiments on the influence of soil type on burrowing activities of worms which confirmed those of Dr Satchell, and E. Gorham commented that the importance of differentiating between soils of pH about 5 and above, and those of about 4·5 and below was borne out by differences in other soil properties occurring at about this point. Other points were raised by T. T. Macan, W. B. Yapp, J. E. Peachey and F. Raw.

Mr J. G. Blower next gave an account of the distribution of British millipedes in relation to the base status of the soil.

Millipedes of the orders Nematophora and Polydesmoidea are mainly surface-dwelling species characteristic of the woodland floor which offers suitable microhabitats. By contrast, the Iuliformia and the pill millipede *Glomeris* are burrowing animals and some of these extend their range into grass and arable land. Examples from this last group were considered since their distribution immediately eliminates vegetation cover as a factor in their preference for soils of a particular type.

Preference for either base-poor sandy soils or base-rich clays and loams is shown by closely related species of the genus *Cylindroiulus*. Thus *C. punctatus* and *C. latestriatus* are characteristic of base-poor soils while *C. londinensis* prefers base-rich soils. Among the Blaniul dae, *Proteroiulus fuscus* belongs to the base-poor category, *Blaniulus guttulatus* and *Archiboreoiulus pallidus* belong to the base-rich category. In addition to these true soil species the hemiedaphic species *Tachypodoiulus niger* and *Schizophyllum sabulosum* (closely related genera of the same tribe) show contrasted preferences for base-rich and base-poor soils respectively. The pill millipede, *Glomeris marginata* prefers base-rich soils and is most numerous on shallow calcareous soils. (There is a species on the Continent, however, which is characteristic of base-poor soils.)

Several differences between the two contrasted soil types which could be limiting factors in the distribution of these millipedes were discussed. Differences in the water regime in the two soils and the possible effect of calcium ions on the water relations of the millipedes were considered.

Questions were raised by T. T. Macan, M. W. Holdgate, G. C. Varley, A. S. Watt, E. D. Le Cren, E. B. Worthington and H. N. Southern.

Later in the evening, dinner was provided in the upper dining-room of Queen Mary College and this, together with the soirée which followed, provided a welcome opportunity for members to meet and talk. The Society's thanks are extended to the Professors of Zoology and Botany for inviting the Society to their Departments for the soirée. A number of interesting exhibits were on view, the range of subjects represented being indicated by the following titles: 'Azorean endemics from volcanic refugia' (P. J. Wanstall); 'Whaling in the Azores' (J. E. Forest and J. G. Carthy); 'Sand culture techniques for the determination of mineral requirements in autecological studies' (A. Bradshaw, M. J. Chadwick, R. W. Lodge and D. Jowett); 'Effects of burning and grazing on blanket bog in Co. Fermanagh' (M. Taylor); 'The quadrat technique in fungal ecology' (M. Dick); 'Habitats of British land snails' (J. Madlin and J. E. Morton); 'Animals of the coralline alga zone' (G. Chapman). In addition, members were able to examine a series of exhibits on algal cytology, which had been prepared for a meeting of the British Phycological Society on the preceding day.

On Saturday, 4 January, following the Annual General Meeting (see below), papers were resumed at 11.20 a.m. when Dr E. Gorham discussed 'The influence of daily weather conditions upon chloride, sulphate and other ions in atmospheric precipitation, and their importance for the supply of ions to fresh water'. Dr Gorham gave examples of chemical analyses for hydrogen, sodium, magnesium, potassium, calcium, chloride, sulphate and nitrate ions in precipitation samples collected in the English Lake District and examined the correlations of daily analyses with (*a*) one another, (*b*) the amount of precipitation,

(*c*) wind direction, (*d*) wind velocity, and (*e*) temperature. Highly significant correlations were found between estimates for H, K, Ca, NO_3 and SO_4. Atmospheric pollution appears to supply much of the sulphate in Lake District rain, since it comes largely as sulphuric acid from the south-east. The correlation between Na, Mg and Cl was also extremely close; the proportions between these ions being very similar to those in sea water. Since these ions are supplied mainly from the south-west, in amounts which are greatly increased by high winds, it may be inferred that sea spray is the principal source. The supply of Cl is considerably higher in cold than in warm weather, a phenomenon possibly connected with stormier conditions and greater evaporation over the Atlantic Ocean.

Dr Gorham demonstrated the importance of the atmospheric contribution of ions to natural waters via precipitation, in particular to upland tarns on hard rocks. Sodium and chloride in most surface waters appear to be almost wholly supplied by sea spray, whereas calcium and magnesium bicarbonates are the main products of soil weathering. Sulphuric acid is shown to be the agent chiefly responsible for the low pH values of organic soils in Britain and elsewhere.

In the discussion following this paper, N. Wace referred to high pH values recorded in water from a bog in Tristan da Cunha, situated only half a mile from the sea. Others taking part were N. A. Burges, A. J. P. Gore, D. J. Boatman, O. J. W. Gilbert, A. J. Brook and C. H. Gimingham.

In a paper on 'The importance of humic acids and calcium to soft-bodied invertebrates in fresh water', Mr D. S. Tucker referred to the various possible reasons for the influence of calcium concentrations on the distribution of fresh-water animals, quoting evidence that a concentration of about 20 p.p.m. represents a critical level. He described a survey of the fauna of molluscs, leeches, flatworms, *Gammarus* and *Asellus* in 15 ponds having calcium concentrations ranging between 6 and 45 p.p.m., and, as a control, one having very hard water. In water containing less than 10 p.p.m. (soft water), the fauna was poor and the species poorly represented. Greater variety and abundance were found where the concentration exceeded 20 p.p.m. In the intermediate range, varying numbers occurred, generally associated with the values for dissolved organic matter. However, larger volumes of water with the lower calcium concentrations can support a richer fauna, possibly because humic acids do not accumulate to the same extent as in smaller ponds. The rate of mortality of *Dendrocoelum lacteum* was shown experimentally to be directly related to the concentration of humic acids.

Comments were made by E. Gorham, O. J. W. Gilbert, T. B. Reynoldson, J. G. Skellam, Miss M. Shaw and F. Raw.

Following lunch, the series of papers was continued by Dr D. J. Boatman whose subject was '*Schoenus nigricans* in the west of Ireland'. A comparison was made between the 'yield' and cation content of the leaves of *Schoenus* and the cation content of the peat in which it was growing. Three types of habitat on the Galway-Mayo Peninsula were sampled: (1) flushes receiving drainage from neighbouring rock ridges, (2) *Sphagnum*-dominated areas, and (3) true blanket bog with amorphous peat.

A relationship was demonstrated between 'yield' and the total exchangeable bases (Na +K+Mg+Ca+Fe). However, a closer relationship was shown to exist between 'yield' and the product of the concentrations of potassium and calcium in the peat. It was suggested that the calcium concentration might strongly influence the uptake of potassium which in turn affects the 'yield'.

The bearing of these results on the 'sea spray' hypothesis was then considered. It was shown that the product of the concentrations of potassium and calcium in the peat of the Galway and Mayo bogs was very little higher than that for other areas of blanket bog from which *Schoenus* is absent. The magnesium concentration was, however, much higher and it was suggested that this might be responsible for enabling the plant to survive on bogs in this region. Nevertheless, the cation content of these Irish peats is equivalent only to the type of peat on which 'poor fen' develops in Sweden. Other types of habitat in which the plant thrives in the west of Ireland were mentioned and it was pointed out that the plant grows where the oxygen content of the peat would be expected to be high. It was also suggested that the plant might be able to tolerate only a narrow

range of conditions in the seedling stage and that these conditions were well represented in the region in question.

E. Gorham opened discussion on this paper by showing slides which suggested that the occurrences of *S. nigricans* in 'acid' ombrogenous bog were mainly concentrated in western regions where the climate was particularly equable, but Dr Boatman drew attention to its absence from large areas of bog in the even more favourable climate of Kerry. P. J. Newbold suggested the existence of genetic difference between Irish and British populations of the plant, while N. Wace raised the possibility of a wider ecological amplitude in Ireland resulting from fewer competitors. V. M. Conway reported failure to establish it on peat at Moor House.

A study of the nutrient requirements of *Molinia caerulea* and *Eriophorum vaginatum* was next described by Mr A. J. P. Gore under the title 'Some aspects of blanket peat fertility'.

Blanket peat at Moor House (National Nature Reserve) is thought to be less fertile than peat from Roudsea and High Newton in north Lancashire. *Eriophorum vaginatum* is co-dominant with *Calluna vulgaris* at Moor House; it occurs with much less frequency at the other two places which are notable for an abundance of *Molinia caerulea*. It was postulated that *Molinia* requires a higher mineral nutrient status than *Eriophorum vaginatum*. At Moor House with its complete absence of *Molinia* the total nitrogen of the peat is significantly lower than at either Roudsea or High Newton, but in other respects analytical results were essentially similar.

Boxes of peat were transferred so that all three types were represented in each of the three environments. Seedlings of *Eriophorum vaginatum* were grown on the peats and harvested as complete plants after one season's growth. Under similar conditions the average dry weight of plants grown on Roudsea peat was in all cases higher than that of plants from Moor House peat; this, however, was not the case on High Newton peat.

Changing the pH from about 3·0 to 5·0 and raising the phosphate concentration in field plots at Moor House, failed to produce any improvement in growth in either species. However, removal of plants and the associated peat so treated to a greenhouse resulted in rapid increase in leaf growth. Addition of mineral nitrogen to plants and peat similarly removed but not previously treated also resulted in a marked improvement in leaf development. No response was observed in untreated controls. Pot experiments in the greenhouse using peat from Moor House showed that in comparison with untreated controls, growth was improved both by nitrogen alone and by phosphate alone. However, phosphate-treated plants were chlorotic, whereas nitrogen-treated plants were dark green.

It appears that available nitrogen is the nutrient factor most limiting plant growth on blanket peat at Moor House. Furthermore there is a strong possibility that his deficiency of nitrogen is critical for *Molinia caerulea* but not for *Eriophorum vaginatum*.

P. J. Newbold mentioned work by Tamm which showed a response by *E. vaginatum* to added phosphate; and other points, including the influence of atmospheric pollution and moor burning on nitrogen supply, were raised by J. L. Harley, E. Gorham and V. M. Conway.

The final paper, by Dr J. M. Boyd, was concerned with the ecology of the Lumbricidae in the shell-sand-peat complex of the Hebrides.

The mineral base of the soils of Islay, Tiree, Coll and the Outer Hebrides is composed of erosion products from Lewisian and Torridonian rocks, together with materials taken from the sea and deposited in the form of shell-sand on windward coasts. The soils composed mainly of erosion products are acid, and those of marine products basic. Along lines at right angles to the coast there is in many places a wide range in soil conditions from calcareous sand to peat, in distances of about 1 km. Dr Boyd described an investigation along such a gradient of the distribution of the Lumbricidae, a group known to be affected by pH, available calcium content and moisture content of the soil. The seventeen species were divisible into groups living in the main ecological zones of the soil habitat: dunes, *machair*, cultivated land, grass-moor and heather-moor. The abundance of the species was related to soil type.

The ecological discontinuity caused by a stock-proof fence affected the distribution of

the earthworms. Species which are abundant on the cattle-grazed pastures on one side of the fence, are relatively scarce on the ungrazed ground; while one species found in abundance on the ungrazed ground is absent on the grazed. This can be explained more readily on a basis of moisture than on pH. On a highly uniform type of grassland some species are seen to aggregate in and around dung-pats, while others seem not to do so. This can be explained on a basis of food supply, though pH may play a part.

J. E. Satchell and R. E. Parker commented on matters arising from this paper.

At the close of the meeting, the President expressed the Society's warmest thanks to the Principal of Queen Mary College for the hospitality shown by the college and for the use of halls and provision of excellent meals. All members attending the meeting had appreciated the admirable arrangements, and on their behalf gratitude was expressed to the Professors of Botany and Zoology, and to Mr P. J. Wanstall who, as local secretary, had done so much to make the meeting a success.

THE ANNUAL GENERAL MEETING

The 39th Annual General Meeting of the Society began at 10 a.m. on 4 January. The following are the (unconfirmed) Minutes of this meeting.

MINUTES OF 39TH ANNUAL GENERAL MEETING

The President, Professor G. C. Varley, took the chair in the Stern Hall, Queen Mary College, University of London, at 10 a.m. on 4 January 1958.

(1) The Minutes of the 38th Annual General Meeting having appeared in *J. Ecol.*, **45**, 3 and being due to appear in *J. Anim. Ecol.*, **26**, 2, were taken as read and were approved.

(2) The Report of the Honorary Secretaries for the year 1957 was read by Dr C. H. Gimingham, as follows:

Report of the Honorary Secretaries

The 38th Annual General Meeting of the Society was held in the Meeting Rooms of the Zoological Society of London at Regent's Park, London, at 10 a.m. on 8 January 1957. The chair was taken by the President, Professor G. C. Varley. An account of the proceedings has appeared in *J. Ecol.*, **45**, 3 and will appear in *J. Anim. Ecol.*, **26**, 2.

On the preceding afternoon papers had been read by Dr J. Warren Wilson, Mr M. E. Solomon and Mr T. O. Pritchard. Later, instead of the more usual soirée, an informal dinner was held in the Fellows' Restaurant of the Zoological Society, and was much enjoyed by all present. The presidential address on the subject 'Ecology as an experimental science' followed the A.G.M. on the morning of 8 January and appears in full in both of the Society's Journals. The afternoon was devoted to papers by Mr P. Greig-Smith, Mr E. Broadhead and Dr J. L. Harper (in collaboration with Mr T. W. Ludwig). The Society's thanks are extended to the Council of the Zoological Society for their hospitality and the excellent facilities provided in their Meeting Rooms and restaurant. Members were invited by the Shell-Petroleum Co. to a showing of films of biological interest in Shell-Mex House, following the meeting.

The Spring Meeting took place in Cambridge on 27-29 March, when members were most comfortably accommodated in the Garden Hostel at King's College, and were able to delight in the prospect of the 'Backs' at daffodil-time on their way to and from the meetings in the Department of Zoology. A soirée was held in the Audit Room of King's College on the evening of 27 March, and the following day Dr G. Salt, Mr R. W. J. Keay, Mr E. J. Moynahan, Mr R. Bainbridge, Mr R. C. Fisher and Dr H. B. Cott contributed papers, and demonstrations were on display in the laboratory. On the morning of 29 March the Hon. Treasurer opened the proceedings with his Report on the Society's finances for 1956. Then followed further papers by Dr J. L. Cloudsley-Thompson, Miss J. Harker, Dr A. J. Rutter (in collaboration with Mrs K. Sands) and Dr G. C. Evans, and some members were later shown the controlled environment cabinets constructed in the Botany School. On the final afternoon excursions took place to the Ornithological and Entomological Field Stations. The welcome extended by the Zoological Department,

and the kindness of the authorities at King's College in providing accommodation are gratefully recorded, with particular thanks to Dr G. Salt who made the local arrangements.

Exeter was the centre of the Summer Meeting in July. Between 10 and 15 July excursions took place to Dawlish Warren, Yarner Wood and Knighton Heath, Braunton Burrows, Wistman's Wood (Dartmoor), Dowlands Landslip (Lyme Regis) and the Plymouth Marine Laboratory, thus providing a most varied and stimulating programme. All members present were unanimous in their praise of the arrangements made by Mr T. J. Wallace, and of the way in which he and various helpers led the excursions. With the exception of the first day, fair weather survived until the end of the meeting, after which it succumbed for the remainder of the summer. It is a pleasure to thank the University of Exeter for their invitation and for the amenities of Mardon Hall; and the Professors of Botany and Zoology for their hospitality at a soirée in the Hatherly Biological Laboratories, where also films were shown on the evening of 13 July.

While these three meetings were well attended (over 150 at the Winter Meeting, 40 in the Spring and 60 at the Summer Meeting) it is regretfully recorded that arrangements for an Autumn Meeting to be held from 20 to 23 September at Port Erin, Isle of Man, had to be cancelled owing to the extremely small number of bookings.

The year has marked a change in the frequency of appearance of the *Journal of Ecology*, Volume **45** of which consisted of three parts. No. 1 has 342 pages and contains 16 original papers, 2 book reviews and 3 Biological Flora accounts; No. 2 has 294 pages, 16 original papers, 4 book reviews, accounts of meetings of the Society held in 1956, and 1 contribution to the Biological Flora; and No. 3 has 372 pages consisting of 16 original papers, 4 book reviews, an account of the Annual Meeting, 1957, and 1 contribution to the Biological Flora. The parts of the Biological Flora published in this volume are *Ranunculus acris* L., *R. repens* L. and *R. bulbosus* L., all by J. L. Harper; *Senecio jacobaea* L. by J. L. Harper and the late W. A. Wood; and *Allium ursinum* L. by T. G. Tutin. As a result of decisions taken in 1956, five volumes (Nos. 32, 35, 36, 37 and 38) of the *Journal of Ecology* have been reprinted during the year. As a result of this, complete sets of volumes as far back as Vol. **18** (1929) are now available for sale. Sales of current and back-numbers of both Journals have increased and the Council have ordered further increases in the numbers of copies printed so that adequate stocks of back-numbers will be laid down. This reprinting has necessitated a considerable reduction in the Society's money investments, but the Council consider that back-numbers of the Journals are a more valuable investment than gilt-edged stocks.

No. 2 of Volume **25** of the *Journal of Animal Ecology*, delayed from 1956, appeared early in the year, containing 282 pages, 13 original papers, reviews of 5 books, abstracts and reports of meetings. At the present time, No. 1 of Volume **26** has been published with 246 pages, 9 original papers, reviews of 6 books, abstracts and reports on the meetings in 1956. The continued larger size of the Journal has enabled the Editor to reduce the time between receipt of a manuscript and its publication to the minimum practicable —between five and eleven months. Sales to non-members both of current and back-numbers have increased in spite of the increases in the sales prices made at the beginning of the year.

Last year the Secretaries recorded their 'confident expectation' that during 1957 membership would pass the 1000 mark. This prediction has proved accurate, the membership now standing at 1010, and a milestone in the history of the Society has thus been passed. Of this total 166 members take both Journals, 512 the *Journal of Ecology* only and 309 the *Journal of Animal Ecology* only. There are 18 Associate Members and 5 Honorary Associates. During the year, 86 new members have been elected, and while 50 deaths and resignations have been recorded the steady increase in numbers of members may be taken as a sign of the health of the Society and an increasingly widespread interest in Ecology. Some 330 members reside overseas.

A circular dispatched to all members in October, warning of the impending increase in subscriptions, brought in its wake about 37 resignations, while 18 members previously subscribing to both Journals are now receiving one only. On the other hand, 9 have changed from one to both Journals, and the Officers and Council are encouraged by the

small number of resignations following upon the announcement to feel that members support them in the view that the increase, avoided for so long, is now inevitable, and that the Journals, meetings and other facilities of the Society continue to provide good value for the amount of the subscription.

Renewed effort has been made to bring the most recent printed list of members and their addresses as up to date as possible. Members are asked to scrutinize this list regularly and to inform the Secretaries of any alterations required.

Both the Council and the Standing Committee on Publications have met three times during the year to conduct their usual business of electing members, planning future meetings and activities and administering the Journals.

The Society was represented by Professor Pearsall at the unveiling of a tablet erected by the Nature Conservancy at Kingley Vale, West Sussex, in memory of A. G. Tansley.

C. H. GIMINGHAM
E. D. LE CREN
31 December 1957 *Honorary Secretaries*

On the motion of Mr H. C. Gilson, seconded by Professor A. R. Clapham, the report was adopted.

(3) Mr V. S. Summerhayes presented the provisional report of the Hon. Treasurers. While at this stage it was impossible to give a full account of the year's working, Mr Summerhayes pointed out that by the end of the year the Society's reserves were virtually exhausted and that henceforward it would be necessary to meet all expenditure from income. In view of the increased subscription and continuing increases in sales of Journals and of back-numbers he was hopeful that this would present no serious difficulty.

On the motion of Dr A. S. Watt, seconded by Dr J. M. Lambert, it was agreed to renew the grants of £10 to the Freshwater Biological Association and £2 2*s*. to the British Committee for International Nature Conservation.

Professor A. R. Clapham's proposal that the Auditors, Messrs Ryland, Clift & Co., be reappointed for the ensuing year was also agreed.

(4) Council's nominee for election to the office of President, on the retiral of Professor G. C. Varley, was Professor N. A. Burges, who was unanimously elected. Other officers were elected as follows:

Vice-President: D. A. Webb
Hon. Secretaries: C. H. Gimingham, E. D. Le Cren
Hon. Treasurers: F. H. Whitehead, J. L. Harper
Hon. Editors (*Journal of Ecology*): P. W. Richards, D. E. Coombe
(*Journal of Animal Ecology*): H. C. Gilson

The following Members were elected to Council:

M. Ashby
F. J. Bingley
P. Greig-Smith
L. A. Harvey — To retire in 1962
F. E. Round — To retire in 1960

On assuming the chair, Professor Burges paid tribute to the valuable work done on the Society's behalf by Professor Varley during his term of office, to which in no small measure must be attributed the achievement of a membership roll exceeding 1000. He also extended the Society's warmest thanks to the retiring Treasurers, Mr V. S. Summerhayes and Mr C. E. Hubbard, who had given devoted service to the Society in carrying the ever-increasing burden of financial administration as the Society grew and extended its activities in a period of unstable monetary values.

(5) In presenting the report of the Editors of the *Journal of Ecology*, Professor P. W. Richards commented that the time lag between receipt of manuscript and appearance of a paper was now considerably reduced by the appearance of 3 instead of 2 parts per

annum. On the other hand, many new papers were coming in, and he appealed to authors to study carefully the Notes for Contributors, before submitting their manuscripts.

Mr H. C. Gilson, Editor of the *Journal of Animal Ecology*, was also able to report a reduction in the delays between the receipt and appearance of a paper, as a result of increases in the size of the parts of the Journal. He also reported his decision to reject an offer of a paper, because the substance of its contents had appeared in letters to *Nature* some years previously. The meeting indicated its support of this action.

(6) Dr C. D. Pigott, reporting on behalf of the Hon. Editors of the Biological Flora, mentioned that 6 completed accounts were in hand for future publication, and that a revised Schedule for Contributors was being prepared.

(7) The President announced that Council wished to nominate two members for election to Honorary Membership: Professor W. H. Pearsall and Sir E. Salisbury. Their election was carried with acclamation. It was also announced that Council had elected Dr K. Blackburn to Honorary Associateship.

The Secretary announced that in accordance with requests by several members it was intended that in future all members should be invited to submit nominations for election to Council, intimation being given annually on the circular for the Autumn Meeting.

(8) The President described briefly a proposal for an Ecological Survey of the Burren District of County Clare, Ireland. Council, after careful consideration of the proposal, had agreed that it should be sponsored by the Society and was prepared to approve a small financial grant towards the cost of organizing the survey. A committee, with Professor Clapham as Convener and Professor Webb as Secretary, had been set up to co-ordinate the project, which it was hoped might be started in 1958 although the major part of the work would be spread over the years 1959-61. University Departments of Botany and Zoology had already been circularized to discover whether a sufficient number of ecologists would be interested to participate, and the response was encouraging.

Dr M. W. Holdgate was called upon to give a short outline of the nature of the area and the possible problems for investigation, which he illustrated with colour photographs.

C. H. G.

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(25 JANUARY 1958)

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